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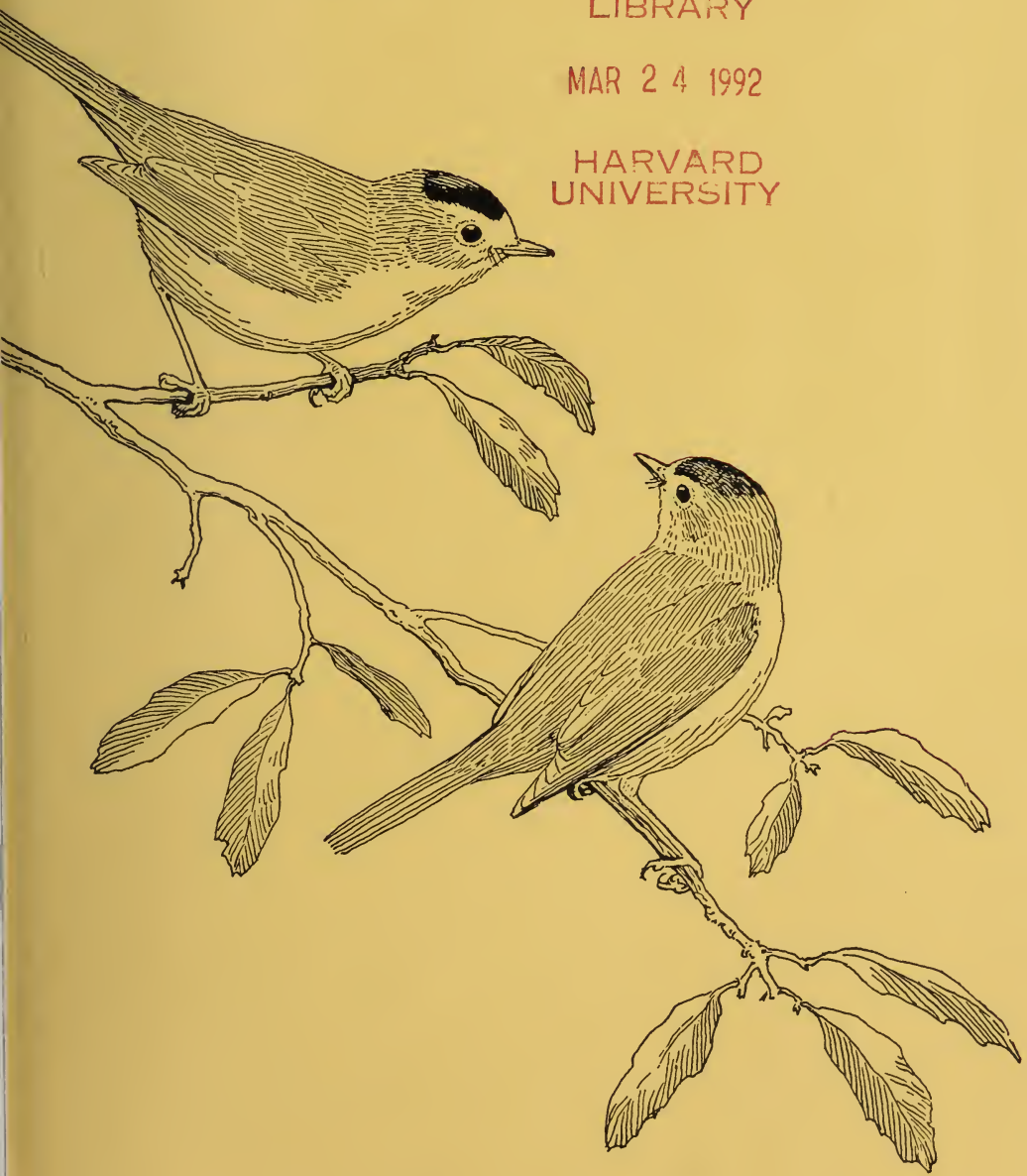

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Seven neotropical ibis species occurring sympatrically in central Venezuela. Top, left to right: Green Ibis (*Mesembrinibis cayennensis*), Scarlet Ibis (*Eudocimus ruber*), White Ibis (*Eudocimus albus*). Center left: Buff-necked Ibis (*Theristicus caudatus*), center right: Glossy Ibis (*Plegadis falcinellus*). Bottom left: Sharp-tailed Ibis (*Cercibis oxycera*), bottom right: Bare-faced or Whispering Ibis (*Phimosus infuscatus*). Painting by Douglas Pratt.

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FORAGING ECOLOGY OF SEVEN SPECIES OF NEOTROPICAL IBISES (THRESKIORNITHIDAE) DURING THE DRY SEASON IN THE LLANOS OF VENEZUELA

PETER C. FREDERICK[1] AND KEITH L. BILDSTEIN[2]

ABSTRACT.—We describe the relative abundance, foraging habitat, and feeding behavior of seven sympatric species of ibises (Threskiornithidae) in the Venezuelan llanos during the dry season of 1989. Scarlet (*Eudocimus ruber*), Glossy (*Plegadis falcinellus*), and Bare-faced (*Phimosus infuscatus*) ibises were the most common species. White (*E. albus*), Green (*Mesembrinibis cayennensis*), Sharp-tailed (*Cercibis oxycerca*), and Buff-necked (*Theristicus caudatus*) ibises together made up less than 8% of individuals surveyed. Multivariate analyses showed that differences in use of foraging habitat partitioned the foraging niche during the dry season, a time when little aquatic habitat is available to the birds. Foraging habitats used by the seven species were differentiated by decreasing distance to water, in the following order: Buff-necked (dry land), Sharp-tailed and Bare-faced (moist soil, occasionally in standing water), Green (water's edge), and Scarlet, White, and Glossy ibises (nearly always in standing water). Probing depth, prey size, and height of vegetation further partitioned the niche. Large differences in capture, probing, and stepping rates were found among all species. There were no differences in foraging behavior or in foraging habitat between congeneric White and Scarlet ibises. Considerable overlap in foraging habitat in space and time was seen among the three aquatic foragers (White, Scarlet, Glossy), and aggression and occasional food robbery occurred among these species. Scarlet Ibises were most aggressive and were most likely to attempt food robbery. *Received 10 Dec. 1990, accepted 26 Sept. 1991.*

Of the approximately 25 species of ibises recognized worldwide (Anonymous 1984), seven occur sympatrically in the central wetland plains, or llanos, of Venezuela. This species diversity is unmatched elsewhere in the world and is sufficient to distinguish the ciconiiform avifauna of the region from that of other Central and North American wetlands (Kushlan et al. 1985). The Scarlet Ibis (*Eudocimus ruber*), White Ibis (*Eudocimus albus*),

[1] Dept. of Wildlife and Range Sciences, 118 Newins-Ziegler Hall, Univ. of Florida, Gainesville, Florida 32611. [2] Dept. of Biology, Winthrop College, Rock Hill, South Carolina 29733, and Belle W. Baruch Institute for Marine Biology and Coastal Research, Univ. of South Carolina, Columbia, South Carolina 29208.

Green Ibis (*Mesembrinibis cayennensis*), Bare-faced or Whispering Ibis (*Phimosus infuscatus*), Sharp-tailed Ibis (*Cercibis oxycerca*), Buff-necked Ibis (*Theristicus caudatus*), and Glossy Ibis (*Plegadis falcinellus*) all occur in the llanos (Gochfeld 1973, Blake 1977, Meyer de Schauensee and Phelps 1978, Thomas 1979). Although the Scarlet and White ibis, when sympatric, are known to interbreed regularly (Ramo and Busto 1987), they are not formally recognized as a single species (AOU 1983). The breeding ecology and life-histories of the Scarlet, White, Bare-faced, and Glossy ibises in the llanos are reasonably well known (ffrench and Haverschmidt 1970, Blake 1977, Meyer de Schauensee and Phelps 1978, Luthin 1983). Little is known of the basic life histories of the other three species (Archibald et al. 1980, Luthin 1983, Ogden and Thomas 1985, Thomas and Strahl 1990). Previous work on the best-studied of the species, the Scarlet Ibis, has concentrated on breeding ecology and distribution during the wet season (ffrench and Haverschmidt 1970; Spaans 1975, 1990; Luthin 1983; Ramo and Busto 1988; Bildstein 1990; Brouwer and van Wieringen 1990; Hislop and James 1990; van Wieringen and Brouwer 1990).

The foraging ecology of this guild is of interest for several reasons. First, the diversity of ibis species in the llanos raises questions of niche separation and behavioral foraging competition among sympatric species. Foraging niche characteristics of all seven species have been summarized qualitatively by Kushlan (1978), Ogden and Thomas (1985), and Kushlan et al. (1985). However, quantitative comparisons are lacking. Kushlan et al. (1985) suggested that similar foraging behavior and habitat use among these ibis species was likely, particularly during the dry season when receding surface water greatly reduces both potential foraging habitat and the number of prey species available. In contrast, Ogden and Thomas (1985) suggested that considerable partitioning occurred through differential use of microhabitat and probing depth during the dry season.

Second, considerable variation has been noted in the timing, numbers, and location of breeding in Scarlet, White, and Bare-faced ibises (ffrench and Haverschmidt 1970, Kushlan 1977a, Ramo and Busto 1988, Bildstein 1990, Bildstein et al. 1990, Spaans 1990). An understanding of dry season foraging ecology may contribute to an understanding of species-specific breeding parameters and, eventually, to the conservation of these species (Archibald et al. 1980, Luthin 1983, Morales 1990, Bildstein 1990).

Here, we summarize behavioral observations and counts of mixed-species foraging flocks of ibises made at 166 locations in the central llanos of Venezuela during the dry season of 1989. Specifically, we describe relative abundances and foraging behavior of each of the species, intra- and interspecific competitive interactions, foods eaten, social interactions, foraging habitats used, and flock dynamics.

METHODS

Data were collected from 26 March 1989 to 15 April 1989 in the llanos of Venezuela, a large seasonally inundated tropical savanna (Sarmiento 1984), near the end of the dry season when surface water was confined to rivers, irrigation impoundments, natural ponds, roadside borrow pits, and oxbows. Observation sites and survey routes were located between Calabozo, San Fernando, and Bruzual in Apure state. We conducted surveys to determine species composition of foraging flocks at 166 locations along approximately 300 km of trails, roads, and highways, stopping whenever we saw ibises. Counts were made only once along each portion of the route; sizes of flocks, kinds of foraging associates, and numbers of individuals of each species were recorded during each observation. We defined foraging flocks as two or more birds foraging within 50 m of each other; singletons were birds foraging at least 50 m from other ibises. We believe our survey counts were representative of ibis populations in the llanos during the 1989 dry season because the roads we used traversed a wide variety of habitats, and because roadside ponds, ditches, and borrow pits are the last concentration points for birds during the dry season (Thomas 1979).

A number of areas along the same survey route were repeatedly sampled for (1) prey types captured and handling time of prey items (2 locations, 4 days), (2) activity as a function of time of day (96 locations, 17 days), and (3) foraging flock associates (110 locations, 11 days).

The foraging behavior of individual birds was sampled using 4-min focal observations of individuals (cf, Bildstein 1983). During each observation, a focal bird was watched through a 15–60× telescope or 10× binoculars, and its behavior recorded on a tape recorder. Recordings were transcribed within two days of each observation. The duration of each behavioral pattern was timed by stopwatch during transcription, and the number of steps, probes, gapes, lookups, captures, and aggressive interactions counted for every focal bird. Probes were typified by a forward and downward thrust of the bill into the water or substrate (Kushlan 1978, Petit and Bildstein 1987). During gapes (=head swinging, sensu Kushlan 1978) the bill was held slightly open and was swept with a side-to-side motion through the water in an arc pivoting about the birds' legs. Lookups were defined as an alert, nonfeeding posture with head held upright for >3 sec. Focal samples that included >30 sec of lookups (N = 16) were not used in our summaries of foraging rates. Captures were readily identified by a distinctive backward jerk of the head accompanied by swallowing motions. Prey size was estimated as a fraction of bill length or gape width, which, in turn, were measured on museum specimens.

For each focal sample, we recorded flock size and composition, distance to surface water, distance to and species of nearest neighbor, vegetation type and height, and foraging habitat type. Height of vegetation and depth of water were estimated in fractions of tarsometatarsal length, based on mean measurements from museum skins. Overall, we recorded the foraging behavior of 484 birds in 37 locations on 19 days of observation. Intra- and interspecific comparisons were made possible by taking focal observations of two individuals (a paired observation, sensu Petit and Bildstein 1987) in the same flock, either simultaneously by two different observers or within 10 min of each other by a single observer.

We used three types of multivariate analyses to determine the extent of differences among the seven species, using data from the 4-min individual observations of foraging behavior. Species was the dependent variable in all cases, with flock size, numbers of species in the flock, depth of water, height of vegetation, distance to water, time spent looking up, and numbers of steps, probes, captures, lookups, and gapes as independent variables. Because variance increased with sample size for all independent variables, data were log-transformed prior to analysis. All analyses were performed using the PC-SAS statistical analysis package (SAS Institute 1985).

Canonical variates analysis determines which linear combinations of variables best sep-

arate two or more groups. We used this method in an attempt to describe sources of variation among species and to reduce dimensionality for other analyses (James and McCulloch 1985). We also performed a multiple analysis of variance (MANOVA) to look for specific differences among the centroids of species along multivariate axes. Finally, we used discriminant function analysis to evaluate the use of the habitat and behavioral variables in distinguishing among species through reclassification.

RESULTS

Species composition.—Scarlet, Glossy, and Bare-faced ibises (in that order) were by far the most common species of ibises seen in surveys (92% of all individuals, Table 1). The other four species made up a total of less than 8% of the ibises seen. Juveniles and sub-adults made up 13% of the Scarlet Ibises seen (Table 1); small sample sizes and lack of a distinctive juvenal plumage precluded the determination of age composition in the other species.

Size of foraging flocks and numbers of foraging associates.—Buff-necked and Sharp-tailed ibises were usually found in small, conspecific flocks, often well away from other species (Table 2). Flocks of Buff-necked Ibises usually comprised 2–6 individuals, with courtship activities seen in more than half of the flocks. We found three active nests of this species in the vicinity of Hato El Frio near Mantecal between 11 and 14 April, suggesting that at least small numbers of Buff-necked Ibises breed late in the dry season (Ogden and Thomas 1985). Buff-necked Ibises were more likely to be found in single-species flocks and as singletons than other species, and this species had the greatest mean nearest-neighbor distance (Table 3).

Despite a tendency for Sharp-tailed Ibises to feed in small single-species flocks with large nearest-neighbor distances, individuals of this species rarely foraged as singletons (2.9% of flocks, the lowest of any species). Forty-two percent of the Sharp-tailed Ibis flocks we saw (N = 24) were composed of two adults, often of discernibly different body sizes and facial coloration, suggesting the individuals were male-female pairs (Blake 1977). Twenty-five percent of Sharp-tailed Ibis flocks also included a third, notably smaller individual, with relatively drab and undeveloped facial coloration, possibly a juvenile (Luthin 1983). We observed frequent calling among presumptive pair and family members, as well as gentle bill-pecking of the larger birds by smaller individuals, sometimes followed by allopreening of smaller birds by the larger individuals.

Glossy, Bare-faced, and Scarlet ibises were consistently seen in larger flocks than were the other species. All three species were frequently found with other species of ibises (Table 2) as well as with domestic animals (Table 3), and White, Glossy and Scarlet ibises were often found feeding near other species of waterbirds (Table 3). Bare-faced Ibises, which often associated with other species of ibises and domestic animals, almost never

TABLE 1

NUMBERS OF IBISES SEEN ON SURVEYS DURING THE DRY SEASON IN THE VENEZUELAN LLANOS (NUMBERS EXPRESSED IN PARENTHESES ARE PERCENTAGES OF TOTAL BIRDS SEEN ON SURVEY)

	Species[a]								
	SCIB								
Survey route	Adults	Juveniles	WHIB	GLIB	GRIB	BFIB	BNIB	STIB	Total
Calabozo to San Fernando[b]	84 (30)	31 (11)	2 (07)	4 (1)	56 (20)	84 (30)	17 (6)	5 (2)	283
San Fernando to Bruzual	299 (30)	25 (3)	15 (1)	474 (47)	0 (0)	187 (18)	10 (1)	2 (0.2)	1012
Entire route	383 (30)	56 (4)	17 (1)	478 (37)	56 (4)	271 (21)	27 (2)	7 (1)	1295 (100)

[a] SCIB = Scarlet Ibis, WHIB = White Ibis, GLIB = Glossy Ibis, GRIB = Green Ibis, BFIB = Bald-faced Ibis, BNIB = Buff-necked Ibis, STIB = Sharp-tailed Ibis.
[b] The survey route is divided to reflect potential differences in species composition from differences in habitat between the central (Calabozo–San Fernando) and western (San Fernando–Bruzual) sections of the llanos.

TABLE 2

SUMMARY OF THE FLOCKING BEHAVIOR OF SEVEN SPECIES OF IBISES DURING 4-MIN FOCAL OBSERVATIONS IN THE DRY SEASON IN THE VENEZUELAN LLANOS

Species	No. flocks	Mean no. ibises in flock (sd)[b]	Mean no. conspecifics in flock (sd)	Percent of flocks of focal species containing:[a]						
				SCIB	WHIB	GLIB	GRIB	BFIB	Conspecifics only	Single bird
SCIB	271	17.64 (45.82)	15.30 (45.04)	100	11	36	26	26	35	13
WHIB	55	4.10 (1.99)	1.76 (1.68)	91	100	58	27	36	6	6
GLIB	132	26.17 (62.87)	12.34 (41.19)	76	24	100	33	28	59	16
GRIB	143	9.13 (11.54)	2.73 (2.60)	50	11	30	100	30	29	13
BFIB	161	15.48 (47.45)	3.67 (6.18)	44	12	23	27	100	39	19
BNIB	24	6.83 (8.74)	2.54 (1.78)	21	8	13	21	21	71	21
STIB	31	5.58 (7.82)	1.97 (0.07)	13	3	10	26	19	52	3

[a] Compiled from flock censuses and ad lib behavioral samples of flocks.
[b] Total numbers of individuals of all ibis species in flock. Does not include numbers of other waterbirds present and does not count the focal individual.

TABLE 3

SUMMARY OF NEAREST-NEIGHBOR ASSOCIATIONS IN FEEDING FLOCKS OF SEVEN SPECIES OF NEOTROPICAL IBISES, SHOWING NEAREST-NEIGHBOR ASSOCIATIONS AND MEAN NEAREST-NEIGHBOR DISTANCES

	Focal species						
	SCIB (N = 50)	WHIB (N = 12)	GLIB (N = 14)	GRIB (N = 36)	BFIB (N = 20)	BNIB (N = 44)	STIB (N = 19)
Nearest neighbor species							
SCIB	72[a]	92	43	8	8	2	0
WHIB	1	0	0	0	0	0	0
GLIB	8	0	57	0	3	0	5
GRIB	0	0	0	9	0	2	5
BFIB	6	8	0	0	83	5	21
BNIB	0	0	0	0	0	91	0
STIB	2	0	0	0	6	0	68
Nearest neighbor Distance (m)							
Mean	2.4	2.4	1.4	4.2	3.4	8.2	6.6
SD	3.79	1.97	0.64	4.97	2.95	8.88	8.25
N	45	11	11	19	32	35	17
Flocking Associates (% of flocks)							
Domestic animals[b]	16	17	4	8	18	3	3
Other waterbirds[c]	43	33	73	18	0	16	21

[a] Percent of total nearest-neighbor observations for focal species.
[b] Primarily cattle and horses, occasionally swine or burros.
[c] Primarily White-faced Whistling-Ducks (*Dendrocygna viduata*), Black-bellied Whistling-Ducks (*D. autumnalis*), Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), Rufescent Tiger-Herons (*Tigrisoma lineatum*), Wood Storks (*Mycteria americana*), Jabiru Storks (*Jabiru mycteria*), Cattle Egrets (*Bubulcus ibis*), and Roseate Spoonbills (*Ajaia ajaja*), with occasional Crested Caracaras (*Polyborus plancus*), Horned Screamers (*Anhima cornuta*), Comb Ducks (*Sarkidiornis melanotos*), and Black-necked Stilts (*Himantopus himantopus*).

foraged with non-ibis waterbirds. Glossy, Scarlet, and Bare-faced ibises maintained the smallest nearest-neighbor distances within foraging flocks, with Glossy Ibises occurring most often in conspecific-only flocks, and tolerating the most dense packing. Although White Ibises were almost always associated with Scarlet Ibises (91% of flocks, 92% of nearest neighbors), this species tended to be found in flocks containing fewer birds, and fewer species of ibises than were Scarlet Ibises. Green Ibises usually fed in a dispersed fashion on the periphery of mixed-species flocks, usually with other Green Ibises as their nearest neighbor.

Time of day and feeding activity.—Scarlet and Glossy ibises were more active during the early morning hours than later in the day (Fig. 1), a trend which was not as pronounced in Green Ibises. Bare-faced Ibises showed a peak in activity during mid-day. Although sample sizes were

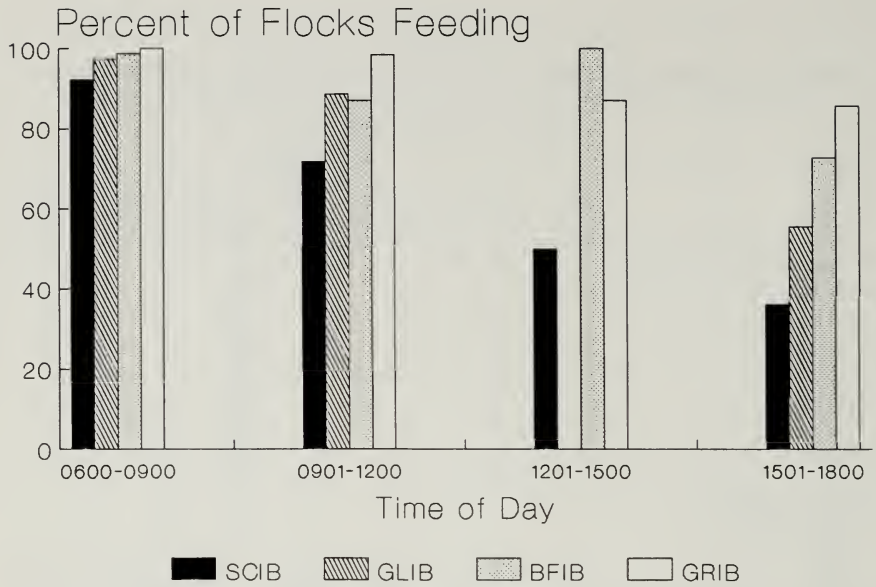

FIG. 1. Feeding behavior of Scarlet, Glossy, Bare-faced, and Green ibises as a function of time of day.

small, Sharp-tailed Ibises also appeared to be most active during the morning, while Buff-necked Ibises seemed to be active at all hours of the day. We did not search for ibises after sundown, and the possibility exists that some species forage at night as well.

Foraging habitat.—All of the sites at which we watched ibises were relatively open, with trees generally spaced at least 100 m apart. Although we checked other habitats on a number of occasions, we never saw ibises foraging in gallery or riverine forest habitats as has been reported for Green and Sharp-tailed ibises during the wet season (Wood 1923, Luthin 1983). Buff-necked Ibises almost always foraged in parched, dusty fields and recently burned areas in relatively short stubble or other low vegetation. Even so, Buff-necked Ibises foraged within 200 m of water. The

→

FIG. 2. Summary of habitat types in which foraging ibises were observed during 4-min focal samples. Esteros are oxbows of permanent or temporary river containing pools of standing water and green vegetation. Ponds were naturally occurring roadside ponds or depressions at least 5 cm deep. Borrow pits were roadside ditches from which large amounts of material had been taken for roadbuilding.

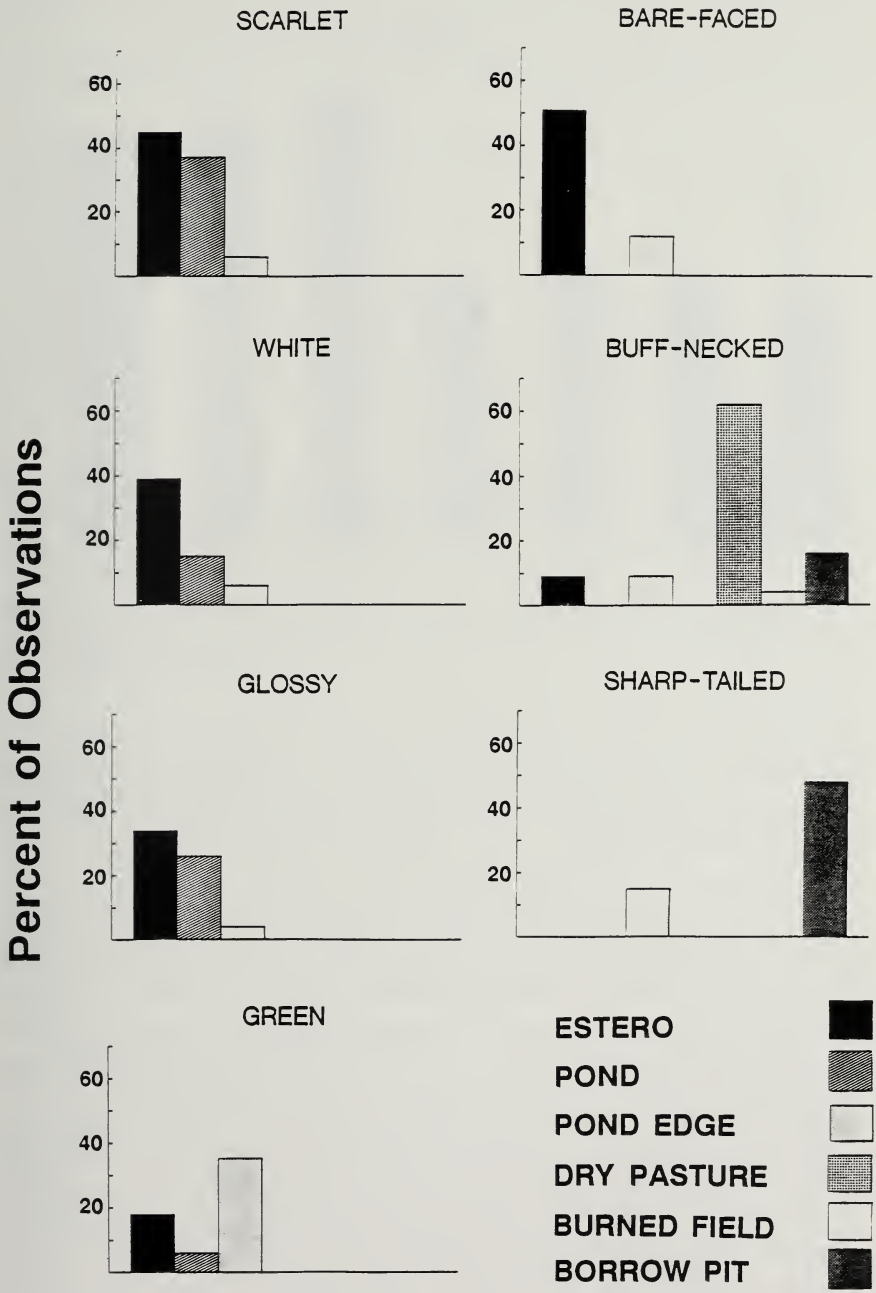
SCARLET
BARE-FACED
WHITE
BUFF-NECKED
GLOSSY
SHARP-TAILED
GREEN
60
40
20
Percent of Observations
ESTERO
POND
POND EDGE
DRY PASTURE
BURNED FIELD
BORROW PIT

TABLE 4
SUMMARY OF FORAGING HABITAT CHARACTERISTICS OF FOCAL INDIVIDUALS[a]

Species	N	Percent of individuals in water	Distance to water (m)	Water depth (cm)	Vegetation height (cm)
SCIB	153	93	3.4 ± 12.7	4.6 ± 3.5	17.5 ± 11.0
WHIB	33	78	10.0 ± 24.1	3.1 ± 2.8	19.6 ± 9.5
GLIB	55	94	0.2 ± 1.0	4.2 ± 2.7	12.8 ± 7.6
GRIB	55	94	11.4 ± 22.1	1.0 ± 1.4	11.4 ± 5.5
BFIB	67	17	63.2 ± 81.8	0.8 ± 1.9	12.5 ± 8.4
BNIB	71	2	122.9 ± 95.8	0.1 ± 0.3	8.3 ± 5.3
STIB	50	46	47.4 ± 78.9	1.6 ± 2.2	6.3 ± 7.7

[a] All values are means ± one SD.

other six species of ibises were more closely associated with moist soil and standing water. Esteros (moist to shallowly flooded oxbow meadows) were commonly used by all species, except Buff-necked and Sharp-tailed ibises. Both Sharp-tailed and Green ibises used the moist edges of pools, ponds, and wetlands, although both species were rarely found feeding in water deeper than 2 cm (Fig. 2, Table 4). Although Green and Bare-faced ibises fed at similar sites, Bare-faced ibises foraged in somewhat taller vegetation than did Green Ibises and were rarely found foraging in water. We noticed an increase in relative numbers of Sharp-tailed Ibises in the flatter and more open south-western llanos, where they often fed in borrow pits that were usually devoid of emergent vegetation. This species seemed to prefer shorter vegetation than did either Green or Bare-faced ibises (Table 4).

Scarlet, White, and Glossy ibises foraged in similar habitats overall (Fig. 2). They often foraged in relatively deep water, and when foraging on dry ground were very close to open water. Scarlet and White ibises were found in somewhat taller vegetation than other species of ibises, although the differences in mean vegetation height were not large among the three aquatic species (Table 4). These three species were distinct from the others in having relatively long legs for their body size (Fig. 3).

Foraging behavior.—Buff-necked Ibises had by far the highest stepping, and lowest probing rates of any species (Table 5). Probing behavior in this species consisted of shallow probes and pecks directed at the surface of the hard, dry substrate. Sharp-tailed Ibises had the second highest stepping rates, the lowest probing efficiencies (captures/probe), low capture rates, and probed more rapidly and deeply than any other species. As a result, then, their bills were often covered with mud to the gape, a

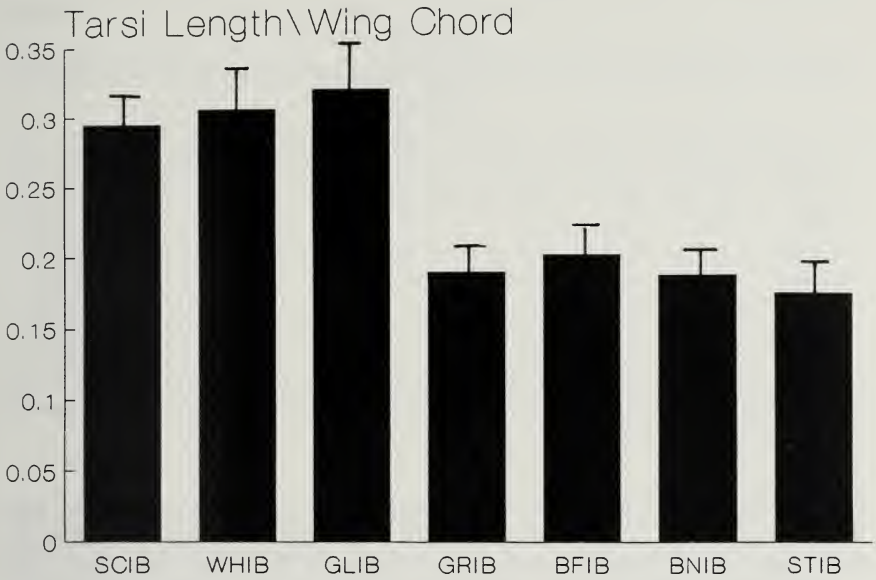

FIG. 3. Mean ratios of the length of tarsometatarsus to wing chord in seven species of ibises. Measurements are from museum specimens collected in the llanos. Vertical lines are + one standard deviation.

phenomenon seen rarely in only one other species, the Green Ibis. Green Ibises showed high capture rates and probing efficiencies, coupled with intermediate rates of stepping and probing. Glossy Ibises had the highest capture rates of any of the species, as well as very high probing rates and probing efficiencies. Glossy Ibises exhibited relatively slow stepping rates because they intensively probed the small area around their bodies. Bare-faced, White, and Scarlet ibises had nearly identical capture and probing rates, although Scarlet Ibises stepped less often than Bare-faced or White ibises.

Comparisons of the foraging behavior of paired White and Scarlet ibises feeding in the same flocks (N = 17 pairs) showed no significant differences (Wilcoxon Matched-Pairs Signed Ranks tests, $P > 0.05$) except for probing efficiency, in which White Ibises were more efficient than were Scarlet Ibises ($P = 0.04$). No significant differences were found in the foraging behavior of paired Glossy and Scarlet ibises (N = 13 pairs).

Multivariate analyses.—All six potential composite variables constructed by the canonical correlates analysis were highly significant ($P < 0.0001$), and no reduction in dimensionality was possible using this analysis. The first three canonical correlates accounted for over 97% of the total vari-

TABLE 5

SUMMARY OF THE MEAN FORAGING RATES OF FOCAL INDIVIDUALS OF SEVEN SPECIES OF IBISES

Species	Steps/ min.	Probes/ min.	Probes/ step	Captures/ min.	Captures/ probe	Captures/ step	Look-ups/ min.	N[a]
SCIB	16.2	34.6	2.2	1.5	0.04	0.10	1.20	124 (10)
WHIB	24.4	34.2	1.4	1.4	0.04	0.06	0.89	30 (7)
GLIB	12.5	41.5	3.3	3.3	0.08	0.27	0.81	48 (5)
GRIB	17.6	30.0	1.7	1.9	0.06	1.06	0.89	58 (9)
BFIB	23.1	35.0	1.5	1.4	0.04	0.06	0.81	60 (10)
BNIB	62.5	26.4	0.4	0.5	0.02	0.007	0.24	32 (17)
STIB	26.7	44.8	1.7	0.7	0.01	0.24	0.54	41 (11)

[a] Numbers of individuals (numbers of sites).

ation in the model and were weighted heavily by habitat variables, and relatively little by behavioral variables. Scatter plots of the seven species along these three axes did not result in distinct separations of species, and are not presented. The overall MANOVA model showed a significant effect of species ($P < 0.0001$), as did all 21 pairwise combinations of species ($P < 0.0001$), indicating that the centroids of each species separate distinctly along the multivariate axes. Each of the habitat and behavioral variables also showed significant effects, with the exception of gaping ($P = 0.226$).

Discriminant function analysis revealed relatively low reclassification ability to species, using the behavioral and habitat variables (Table 6). While the discriminatory abilities of the model were significantly different

TABLE 6

PERCENT OF OBSERVATIONS OF EACH SPECIES RECLASSIFIED CORRECTLY TO SPECIES BY THE DISCRIMINANT FUNCTION ANALYSIS

Species	Percent classified correctly
SCIB	66.6
WHIB	84.4
GLIB	61.2
GRIB	54.5
BFIB	50.0
BNIB	75.0
STIB	51.2
Total percent correct	63.3

TABLE 7
SUMMARY OF SIZES OF PREY EATEN BY SEVEN SPECIES OF NEOTROPICAL IBISES DURING THE DRY SEASON[a]

	SCIB	WHIB	GLIB	GRIB	BFIB	BNIB	STIB
Total captures	866	166	91	482	329	63	103
Percent							
<1 cm[b]	87	93	91	98	98	85	90
>1 cm	11	8	9	1	2	13	10
1–2 cm	4	2	8	1	0	3	3
2–3 cm	1	<1	0	0	<1	0	<1
>3 cm	6	5	1	<1	1	10	6

[a] Compiled both from four-minute focal animal samples and ad lib surveys of flocks.

from a random reclassification scheme ($\chi^2 = 668$, df = 6, $P \ll 0.0001$), only 63% of all observations were classified correctly, and in only White and Buff-necked ibises did the reclassification efficiency exceed 75%.

Prey characteristics.—In most cases, we were unable to identify prey because most items were very small (<1 cm), and were swallowed within 2 sec of capture (Table 7). From their shape, size, and the manner in which they were handled, we believe most small prey items were arthropods, along with small numbers of annelid worms and (in the case of Green and Glossy ibises), small gastropods.

Buff-necked and Scarlet ibises included a greater proportion of large prey in their diets than did the other species (14 and 11% of captures over 1 cm, respectively), while almost all of the diet of Green and Bare-faced ibises consisted of prey <1 cm (Table 7). The most commonly identified large items were hemipteran water beetles (Belostomatidae, Naucoridae, Corixidae) and aquatic beetles (Gyrinidae). Giant water bugs, (3–10 cm) accounted for 90% of Scarlet Ibis captures over 1 cm in length. Because of their large size and escape tactics, giant waterbugs were associated with long handling times and frequent piracy attempts.

Aggressive interactions and prey robbery.—Aggressive interactions were rare among foraging Buff-necked or Sharp-tailed ibises, perhaps because both species tended to feed in dispersed, single-species flocks and family groups (Table 8). Similarly, Green Ibises rarely engaged in aggressive interactions, probably because they rarely came into contact with other species.

Scarlet, White, Bare-faced, and Glossy ibises all were regularly involved in aggressive encounters. Scarlet Ibises engaged in aggression most fre-

TABLE 8

SUMMARY OF AGGRESSIVE TENDENCIES OF SEVEN SPECIES OF IBISES IN FORAGING FLOCKS

Species	Minutes observed[a]	Attacks performed[b]/min	Attacks received/min	Aggression ratio[c]
SCIB:				
Males	460	8.8^{1}	$2.9^{1,2}$	3.09
Females	70	$7.7^{1,2}$	6.0^{1}	1.00
Both sexes	538	8.7^{1}	3.4^{1}	2.52
WHIB:				
Males	60	7.0^{1}	$1.0^{1,2}$	7.00
Females	52	0.0^{2}	8.1^{2}	0.00
Both sexes	122	4.4^{2}	6.4^{1}	0.69
GLIB	194	1.2^{3}	$3.1^{1,3}$	0.40
GRIB	246	$0.5^{2,4}$	1.0^{2}	0.50
BFIB	237	$1.8^{2,3}$	$1.5^{2,3}$	1.17
BNIB	219	0.0^{3}	0.5^{2}	0.00
STIB	171	0.4^{3}	0.0^{2}	0.00

[a] Minutes of observation of focal birds in flocks only.

[b] Column entries with different superscript numbers differ significantly from one another ($P < 0.05$, χ^2 goodness of fit test, 1 df with Yates correction).

[c] Attacks performed/attacks received.

quently and initiated aggressive interactions at higher rates, and in higher proportion than did the other species. Glossy Ibises were particularly unaggressive towards conspecifics, even though this species foraged in tight conspecific groups. On one occasion, we observed a Glossy Ibis foraging for over 30 sec with its neck extended over that of its nearest neighbor.

Despite their close association with Scarlet Ibises, White Ibises initiated aggressive interactions only half as often as did Scarlet Ibises ($P = 0.073$, χ^2 goodness of fit test), and were recipients of aggression twice as often as were Scarlet Ibises ($P = 0.0048$). The species difference is largely the result of the behavior of female White Ibises. Although male Scarlet Ibises, female Scarlet Ibises, and male White Ibises did not differ in rates of aggression, all initiated aggression at significantly higher rates than did female White Ibises (Table 8). Female White Ibises also were recipients of aggression significantly more often than were female Scarlet Ibises.

While Scarlet Ibises were more likely to attack other species, these did not always result in displacement (Table 9). Glossy Ibises attacked and displaced Scarlet Ibises in 18% of their aggressive interactions, and White Ibises displaced Scarlet Ibises in 45% of their aggressive interactions.

TABLE 9

NUMBERS OF AGGRESSIVE INTERACTIONS AMONG SEVEN SPECIES OF IBISES IN FORAGING FLOCKS THAT DID NOT INVOLVE PREY

Recipient	Aggressor					
	SCIB	WHIB	GLIB	GRIB	BFIB	Other[a]
SCIB	52	10	0	3	0	2
WHIB	12	2	0	0	0	0
GLIB	13	0	0	0	1	0
GRIB	5	0	0	0	0	0
BFIB	2	0	0	0	12	0
Other[b]	4	0	0	2	0	0

[a] Includes White-faced Whistling-Duck and Wattled Jacana (*Jacana jacana*).
[b] Includes STIB, Southern Lapwings (*Vanellus chilensis*), White-faced Whistling-Ducks, and Great Egrets.

Scarlet Ibises were socially dominant to Green and Bare-faced ibises. Among species, rates of aggression were negatively correlated with mean nearest neighbor distances ($R_S = 0.75, 0.86$, $P < 0.005$ for initiating and receiving aggression, respectively) (Tables 3 and 8).

Of a total of 158 aggressive intra- and interspecific interactions, 33% occurred when the recipient of aggression had food in its bill or was actively pursuing prey. In 18 of these cases (11% of the total), the aggressor clearly attempted to snatch prey from the recipient. Attempts at food robbery were successful in at least three cases (a minimum success rate of 13%). Scarlet Ibises were the most likely species to attempt food robbery (67% of all attempts), with White (17%) and Glossy (16.6%) ibises being the only other two species to attempt food robbery. All attempts at piracy by Scarlet and White ibises were made by males, and only Scarlet Ibises were successful. Scarlet Ibises were victims of attempted piracy 15 times (83% of the total, 2 females, 10 males), Glossy Ibises twice (11%), and Bare-faced Ibises once (6%).

Food robbery was used by some male Scarlet Ibises more than others. Four individuals at one site attempted to steal giant water bugs on a total of five occasions from Glossy Ibises foraging in groups, and apparently also captured several beetles as a result of the beater effect of the flock. Each of the four Scarlet Ibises also repeatedly chased conspecifics from the flock of Glossy Ibises, suggesting that the pirating ibises were defending the flocks as a resource.

We also observed four Crested Caracaras (*Polyborus plancus*) and one Savanna Hawk (*Heterospizias meridionalis*) closely following mixed-spe-

cies ibis foraging groups, attempting to steal giant water beetles from Scarlet and Glossy ibises. Only one of these attempts was successful, directed at a Scarlet Ibis which had in turn stolen the beetle from a Glossy Ibis.

Other foraging techniques.—Foraging flocks of Scarlet, White, and Bare-faced ibises were over twice as likely as those involving other ibis species to include domestic animals (Table 3), and on several occasions, we noted groups of Scarlet, White and Bare-faced ibises closely (<3 m) following domestic cows and horses, apparently capturing insects disturbed by the animal's footsteps. We also observed Scarlet Ibises closely following flocks of 3–50 White-faced Whistling-Ducks (*Dendrocygna viduata*) on 10 occasions, apparently feeding on aquatic insects disturbed by the ducks. The ibises occasionally pecked at the closest ducks, which appeared to keep the flock moving. Groups of 2–16 White-faced Whistling-Ducks similarly foraged behind individual Scarlet Ibises on four occasions, repeatedly displacing one another to gain a spot immediately behind the ibis.

On six occasions, we noted single Bare-faced Ibises foraging alternately in two areas of less than 1 m^2 each, 2–6 m apart in medium to tall grass on moist ground. Individuals probed intensively in one of the areas for 1–6 min, then walked rapidly to the other site and began probing. Three to five trips between the two sites occurred during each observation. We were unable to identify prey items extracted from these intensively worked sites.

DISCUSSION

Species composition.—The relative abundances of the seven ibis species we report differ little from those found by Kushlan et al. (1985), Aguillera (unpubl. data), and Ogden and Thomas (1985). In all three of the previous studies, Scarlet Ibises were the most abundant, with White, Buff-necked and Sharp-tailed ibises making up a very small percentage of the ibis community. Green Ibises comprised less than five percent of the ibises seen by Aguillera (unpubl. data) and ourselves, and Ogden and Thomas (1985) describe them as common in pairs or small groups. In contrast, Kushlan et al. (1985) reported that Green Ibises represented over 36% of the ibises they observed. This considerable departure from the other studies suggests that the species concentrates in certain areas during the dry season, that Green Ibises leave portions of the area entirely during the dry season, or that other species decrease in proportion seasonally. There is also considerable variation in relative abundances of Glossy Ibises among studies, suggesting a slow increase in the abundance of this species since Gochfeld's first report of abundance (Gochfeld 1973, Kushlan et al. 1985, Aguillera unpubl. data from 1981–1982, this study).

Foraging niche relationships.—Our descriptions of foraging habitat and

behavior confirm earlier reports by Luthin (1983), Kushlan et al. (1985), ffrench and Haverschmidt (1970), Ogden and Thomas (1985), and Brouwer and van Wieringen (1990), and support the idea that these seven species of ibises coexist with considerable partitioning of the foraging resource even during the dry season (Ogden and Thomas 1985). Our multivariate analyses suggest (1) that variation in habitat and behavior is sufficient to separate any species-pair along multivariate axes, (2) overlap in the centroids of species on these axes is too extensive to permit an accurate reclassification using the variables we recorded, and (3) taken together, none of the habitat and behavioral variables we used can be excluded as a significant source of variation among species.

The most obvious mechanism partitioning the feeding niches of ibises during the dry season appears to be habitat. Buff-necked Ibises were the only ibis species that regularly foraged on dry land. This species was rarely seen feeding in standing water, even in the absence of other species. Sharp-tailed Ibises also were distinctive in their use of habitat, almost never being found in esteros or broad areas of open water. Two species-assemblages could be further distinguished along an aquatic-terrestrial gradient. Sharp-tailed, Green, and Bare-faced ibises were often found foraging in moist soil as well as along the edge of standing water. Although each of these three species was occasionally found foraging in water, they did so only when other ibis species were absent, suggesting behavioral avoidance. White, Scarlet, and Glossy ibises were the three species with the largest legs in proportion to wing length, were rarely found out of water, and usually foraged in depths of at least 3 cm. Thus on the basis of habitat alone, the potential for direct competition for food seems limited to the Sharp-tailed–Green–Bare-faced group, and the Scarlet-White-Glossy group.

The three species that foraged in moist, but rarely inundated, areas differed in their use of microhabitats. Bare-faced Ibises were rarely (17%) found foraging in standing surface water, and appeared to be restricted to moist areas. Green Ibises were a water's-edge specialist, being found in shallow water 94% of the time, and nearly always within two meters of the shoreline. Sharp-tailed Ibises fed in moist soil and at the water's edge. Their preference for areas with little or no vegetation may be important in limiting contact with Bare-faced and Green ibises. We suspect that the potential for niche overlap with Green Ibises in water's-edge habitat also is reduced by a noticeable difference in probing depths (first suggested by Ogden and Thomas [1985]), that probably results in the higher proportion of large prey consumed by the deeper-probing Sharp-tailed Ibises. Behavioral avoidance also appears to be an important mechanism for reducing dry-season foraging overlap among the three moist-ground species. Green, Sharp-tailed, and Bare-faced ibises had relatively

high probabilities of foraging in single-species flocks, and all showed large nearest-neighbor distances while feeding.

The three aquatic feeders (White, Scarlet, and Glossy ibises) exhibited fewer differences in foraging habitat use. All three foraged in essentially the same habitats (deep, open water), and all used the same foraging techniques (probing rapidly into the surface layer of substrate). Foraging niche overlap between White and Scarlet ibises, and Glossy Ibises may be a relatively recent phenomenon, if, as Gochfeld (1973) suggests, Glossy Ibises have only become abundant in the llanos during this century. Aggressive behavioral interactions among these three aquatic species were certainly the most noticeable of any species combination, the majority of which (>60%) did not involve disputes over captured or pursued prey. Tendencies to interact aggressively were inversely related to nearest-neighbor distances, possibly as a result of the tremendous reduction in available foraging habitat during the dry season.

Despite incomplete dominance, Scarlet Ibises were clearly more aggressive than Glossy Ibises within the same habitat. The increased aggressive tendency of Scarlet Ibises during feeding appears to be a sexually selected feature of the genus (Rudegeair 1975, Kushlan and Kushlan 1975, Ramo and Busto 1985, Frederick 1987), but may also be of selective advantage during feeding. While we were unable to measure the extent to which Scarlet Ibises might have benefited from food robbery, we suggest that their aggressiveness provides them with access to large prey, both directly via prey robbery and indirectly via defense of groups of heterospecific beaters.

Although Glossy, White, and Scarlet ibises may compete for small, predominantly arthropod prey, Glossy Ibises took fewer large prey than did Scarlet Ibises or White Ibises.

White and Scarlet ibises showed little separation in habitat use, foraging behavior, or size and type of prey eaten. White Ibises foraged in slightly shallower water, more often on dry ground, farther from open water and were generally in smaller flocks than Scarlet Ibises. Despite these differences, White Ibises almost always fed with Scarlet Ibises (over 90% of flocks). Similarly, 92% of nearest neighbors of White Ibises were Scarlet Ibises, and White Ibises were never observed with another White Ibis as their nearest neighbor. Considerable aggression occurs between those two species during foraging, and neither species dominates. While Scarlet Ibises seemed to be more aggressive as a whole, this difference is largely the result of smaller female White Ibises (cf. Kushlan 1977b) being less aggressive than Scarlet Ibises of either sex. Overall, our observations do not suggest that substantial differences exist in the foraging ecology of the two species, supporting the idea that Scarlet and White Ibises in the llanos are races of the same species (Ramo and Busto 1987).

Both Kushlan et al. (1985) and van Wieringen and Brouwer (1990) reported that during the wet season Scarlet Ibises in the llanos often foraged on moist ground that was not inundated by standing water. We almost never saw Scarlet Ibises foraging out of water, suggesting that the dynamics of soil-dwelling prey may limit dry-season foraging to inundated areas. If true, the niche of Scarlet Ibises may be considerably reduced during the dry season. Similarly, the inundated gallery-forest described as foraging habitat for Green and Sharp-tailed ibises during the wet season (Luthin 1983) and those reported here indicate these species also shift foraging habitat with season.

Our observations confirm that the majority of foods eaten during the dry season by all seven species are insects, together with small numbers of anurans, crustaceans, gastropods, and oligochaetes (Ogden and Thomas 1985, Kushlan et al. 1985, Luthin 1983, and Brouwer and van Wieringen 1990). Despite the locally high densities of fishes during the dry season (pers. obs., Kushlan et al. 1985, Morales and Pacheco 1986), we never saw ibises consume fishes, even though the three aquatic species we watched often foraged together with piscivorous storks, herons, egrets, and tiger-herons.

Our observations of courtship and nesting of Buff-necked Ibises in the southwestern llanos confirm that at least one peak of nesting in this species occurs near the end of the dry season (Ogden and Thomas 1985, Aguillera, unpubl. data). This is particularly intriguing, in light of the fact that this species had the lowest rate of captures of any species (0.49/min). It is possible that more productive foraging by this species occurs in habitats (such as burning fields) which were not sampled during our surveys.

Finally, we caution that as our observations were made during a single dry season, our results may not be representative of foraging behavior and habitat use in the wet season (above) or in other years.

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COLOR PLATE

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NESTING SUCCESS IN FLORIDA SANDHILL CRANES

Nancy C. Dwyer and George W. Tanner[1]

Abstract.—Through aerial surveys in 1988 and 1989, 111 Florida Sandhill Crane (*Grus canadensis pratensis*) nests were found on a 60-km² site in northern Polk County, Florida. Mean laying dates were 7 March in 1988 and 25 February in 1989. Overall hatching success was 59% using the Mayfield method; however, recruitment was only 5% in both years. Causes of nest failure included predation, flooding, abandonment, and egg infertility and addling, but the cause of 45% of the failures was unknown. Nesting cranes seemed to habituate to certain forms of human disturbance and nested within 400 m of highways, railroads, and mines; cranes also were tolerant of helicopter flyovers. Even so, investigator visits to nests and development-induced alterations of surface water drainage were implicated in 24% of the nest failures. *Received 24 April 1991, accepted 1 July 1991.*

Most studies of nesting success of Sandhill Cranes (*Grus canadensis*) have involved periodic searches for active nests, with subsequent monitoring of the nest contents (e.g., Thompson 1970, Valentine 1982, Walkinshaw 1982, Bennett and Bennett 1990). The Mayfield (1961, 1975) method is well suited for such studies since most nests are found after initiation or the laying of the first egg. This method reduces the bias associated with the lower probability of finding unsuccessful nests, which are shorter-lived than those that hatch successfully (Miller and Johnson 1978, Klett and Johnson 1982). No published accounts of Sandhill Crane nesting success have included this method to determine hatching success.

We here present data on nest success of the Florida Sandhill Crane (*G. c. pratensis*), a threatened species in Florida (FGFWFC 1974). We also assess the impact of human disturbance, including highways, mining, and nest visits by the investigators, on a local crane population in an effort to improve management decisions regarding the conservation of this species.

STUDY AREA

The study site (60 km²) was located in northwestern Polk County, Florida, approximately 50 km southwest of Orlando in a wetland system known regionally as the Green Swamp. The study area consisted of a mosaic of cypress (*Taxodium ascendens*) and bay (*Gordonia lasianthus, Persea palustris, Magnolia virginiana*) swamps, herbaceous marsh, pine (*Pinus palustris, P. elliottii*) flatwoods, scrub oak (*Quercus* spp.), orange groves, and improved pasture (predominantly *Paspalum notatum*) with scattered oak and pine. Palustrine wetlands accounted for 48% of the total study area, more than half of which wetlands were forested. Marsh habitats included seasonally flooded aquatic bed, emergent, and shrub-scrub wetlands (Cowardin et al. 1979). Elevation varied between 40–47 m above sea level. Sources of human

[1] Dept. of Wildlife and Range Sciences, School of Forest Resources and Conservation, Univ. of Florida, Gainesville, Florida 32611.

disturbance to nesting included an interstate highway (I-4) and a 100-ha sand mine. The subtropical climate of the area consists of wet, hot summers and moist, cool winters. Hurricanes may affect summer and fall weather, while relatively little rain falls during spring. August and September, the wettest months, average 184 mm of rain/month, while November and December, the driest months, average 50 mm/month. The 30-year mean January and July temperatures are 15.3°C and 27.6°C, respectively; the annual average temperature is 22°C (NOAA 1990).

METHODS

We systematically surveyed the study area for nests weekly from 13 January through 18 May 1988 from a helicopter flying 40–90 m above ground. In 1989, surveys were flown from 3 January to 25 April by helicopter and by fixed-wing aircraft flying at 50–150 m above ground. Surveys concentrated on marsh habitat. Active nests, defined as those containing eggs or an incubating adult, were obvious from the air. During each flight we plotted nest locations on aerial photographs. We observed nests every 2–10 days in one of three ways: via helicopter or fixed-wing aircraft overflights, from an elevated vantage point (e.g., tree, ladder, truck, or from a >40 m-distance on the ground), or by approaching on foot, thereby flushing the incubating bird ("nest visit"). During each nest visit, we recorded the location, date, nest contents, incubation stage, water levels 1 m from nest edge, and presence of adults in the area.

Eggs were floated in warm (44°C) iodinized water to determine their age (Westerskov 1950). Newly laid crane eggs lie horizontally on the bottom of the water container, whereas eggs more than 15 days old float with the blunt end about 1 cm above the water's surface. Imitating an adult crane's brood call usually elicited a visible or audible response from the chick within a well-developed egg.

We monitored nests more closely during the expected hatching period so that the fate of eggs could be verified. For successful nests, we calculated date of initiation by subtracting the 30-day mean incubation period (Walkinshaw 1976, 1981, 1982) from the hatch date. Fourteen nests visible from a distance throughout the incubation period were not visited ("undisturbed nests") and were used for comparison with visited nests.

To avoid adverse heating and cooling of eggs during nest visits, we spent less than 5 min at each nest and visited nests from 07:00 to 11:00 h or from 16:00 to 17:00 h; we avoided visiting nests during extremely cool or warm weather or if rain was expected. Because flushing cranes sometimes crack eggs (Valentine 1982), we made noisy approaches to avoid surprising incubating birds.

Since cranes have precocial young, nesting efforts were defined as successful if at least one egg hatched. Evidence for nest success included direct observation of one or two chicks, peeping or pipping eggs, or a combination of length of nesting activity at the site together with the presence of eggshell fragments with detached membranes in the nest bowl. If a nesting effort ended before the eggs were aged and none of the above was observed, the outcome was considered unknown, and the nest was excluded from our analysis of nesting success. To determine nesting success, we employed the traditional (successful nests/all nests) and Mayfield (1961, 1975) methods. The assumption of constant daily mortality, central to the Mayfield method, was tested by dividing the incubation period into three 10-day intervals (early, middle, and late) and calculating mortality rates for each of these stages of incubation; a Bonferroni multiple comparison test was used to compare these rates. We used the Z-statistic to test differences between nesting success estimates (see Hensler and Nichols 1981 for derivations). Renesting within the same breeding season was determined based on the location of nests and knowledge of territorial pairs and the fate of their previous nest.

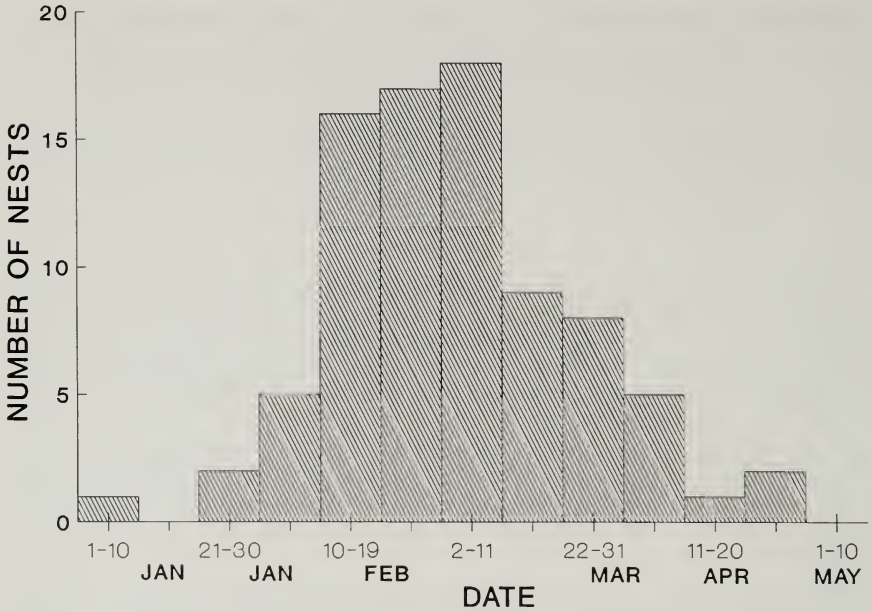

FIG. 1. Initiation dates of 84 Florida Sandhill Crane nests, northwestern Polk County, Florida, 1988 and 1989.

We used both first nests and renests when calculating nesting success statistics. We marked terminated nests with a length of plastic pipe so that we could compare them with subsequent nest locations.

We used evidence remaining at or near the nest to determine which predators affected nesting success (Rearden 1951). We monitored water levels to confirm flooding as a cause of nest failure. Water gauges in 16 wetlands distributed throughout the study area were read every 3–14 days; large marshes contained 4 or 5 gauges as replicates.

In July and August of both years, fledging and recruitment rates were estimated as the percentage of fledglings in roosting flocks of Florida Sandhill Cranes on the study area. We also observed less gregarious pairs or families to help assess the accuracy of ratios in flocks.

RESULTS

Nest distribution and chronology.—Fifty nests were discovered an average of 5.3 ± 0.9 (SE) days after the initiation of egg laying in 1988. In 1989, we found 61 nests an average of 11.0 ± 1.2 days after egg laying, when the average time between surveys was 10.0 ± 0.7 days, compared to 8.0 ± 1.0 days in 1988. In both years mean and median initiation dates were 3 March and 1 March, respectively (Fig. 1). Nests were initiated as early as 2 January (1988) and as late as 22 April (1988). Simultaneously active nests were as close as 72 m. Based on 21 territories that were

TABLE 1
SUCCESS RATE OF 111 FLORIDA SANDHILL CRANE NESTS FOUND IN NORTHWESTERN POLK COUNTY, FLORIDA

	1988	1989
N	47	55
Unknown	3	6
Hatch	66%	69%
Mayfield	59%	59%

assumed to be permanent year-round, pairs nested an average of 124 m (SE = 17.0, range = 8–294) from nest locations of the previous year.

Cranes using wetlands larger than 50 ha nested significantly later ($\bar{x}$ = 59.8 ± 2.3 Julian date, N = 37) than those nesting in wetlands of less than 50 ha ($\bar{x}$ = 53.6 ± 2.9 Julian date, N = 43, $Z = 6.8$, $P = 0.001$). Migrant Greater Sandhill Cranes (*G. c. tabida*) tended to use the larger marshes for foraging.

Hatching success.—Of 102 nests with known outcomes, 69 (68%) hatched at least one chick (Table 1). The Mayfield (1961, 1975) method for calculating nesting success resulted in lower estimates (Table 1). We found no significant differences in mortality rates among early, middle, and late incubation stages ($Z = 0.6$, $P > 0.05$).

Modal clutch size was two eggs ($\bar{x}$ = 1.81). However, 14% (6) and 24% (12) of nests had one-egg clutches in 1988 and 1989, respectively, with a combined success rate of 78%. Nest and egg productivity values were similar between years (Table 2). Of the 75 two-egg clutches with known fate, 53% hatched both eggs, while only one of the eggs hatched in 16% (12) of these nests.

TABLE 2
PRODUCTIVITY, ASSESSED AT THE HATCHLING STAGE, OF FLORIDA SANDHILL CRANE NESTS AND EGGS IN NORTHWESTERN POLK COUNTY, FLORIDA

	1988	1989	1988/1989
Young per egg laid	0.63	0.67	0.65
Young per nest	1.06	1.04	1.05
Young per successful nest[a]	1.61	1.50	1.55

[a] A nest hatching at least one egg.

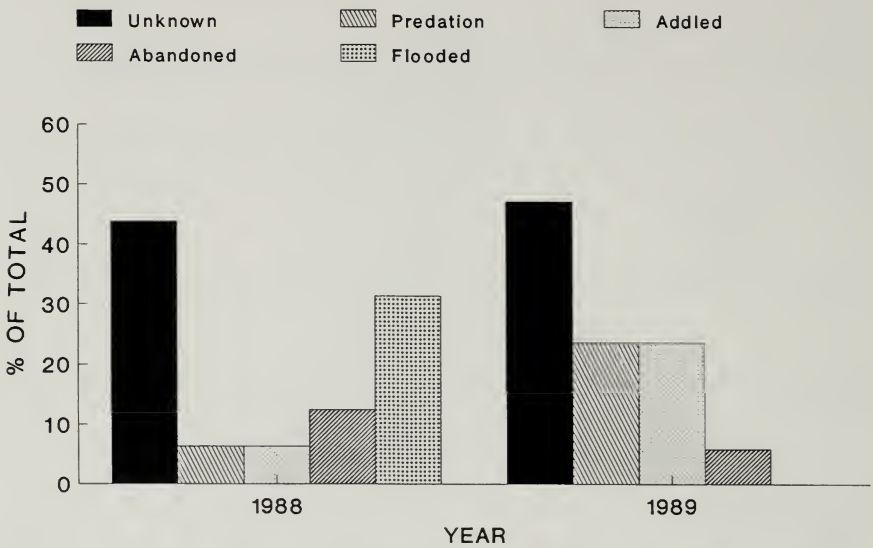

FIG. 2. Suspected causes of nest failure at Florida Sandhill Crane nests in 1988 (N = 16) and 1989 (N = 17), northwestern Polk County, Florida.

Causes of nest failure included predation, flooding, abandonment, and egg infertility and addling (Fig. 2). We often had difficulty ascertaining the exact causes of nest failure, and 15 of the 33 nest failures (45%) were the result of unknown causes. In 1988, the greatest proportion of nest failures (30%, N = 5) was due to flooding between 12 and 22 March. During this period two major rain events rapidly increased average water levels within the wetlands from 15 to 30 cm during this time.

No nests failed due to flooding in 1989; however, nest failures in that year due to addled or infertile eggs and predation were approximately four times as great as in 1988. Although we were unable to identify any predation to species, egg predators common in the area were raccoons (*Procyon lotor*) and Fish Crows (*Corvus ossifragus*). Other nest and chick predators observed on the study area included feral pig (*Sus scrofa*), American alligator (*Alligator mississippiensis*), river otter (*Lutra canadensis*), bobcat (*Lynx rufus*), Red-tailed Hawk (*Buteo jamaicensis*), and Great Horned Owl (*Bubo virginianus*). We observed a Red-tailed Hawk stooping on a pair of cranes and their day-old chick on 25 March 1988.

The three nests that failed due to abandonment during our study probably were associated directly or indirectly to our approach and handling of the eggs and nests during incubation. We attempted to mark a pair of attending adult cranes by securing a sponge saturated with leather dye in

their nest. On the subsequent visit, 9 days later, the eggs were cold and no adults were present.

Chick recruitment.—Based on flock counts in July and August of over 100 communally roosting birds, we found that young-of-the-year represented only 5% of the local population in both years. Apparently, both members of a brood seldom survived. We observed a pair of adults with two nearly fledged chicks on the study site only once each year.

Renesting.—We estimated that 21% of the 111 total nesting attempts were second efforts. Distances between first nestings and presumed renestings averaged 183 ± 62 m, which was closer than the average distance between simultaneously active adjacent nests ($\bar{x}$ = 277 ± 65 m) in the most densely populated marsh. One nest was used twice during the 1988 nesting season.

Human disturbance factors.—Cranes flushed when we were from 3 to 75 m from the nest. Once flushed, the birds remained off the nest for 15 min to at least 3 h.

During surveys, incubating cranes remained on their eggs in 82% (N = 259) of the cases in which the helicopter flew as low as 40 m above them; incubating cranes never flew from the nest during these approaches. Other human activities occurred within 500 m of nest marshes, including citrus harvesting and grove maintenance (including pesticide application), cattle ranching, sand and clay mining, farming, a cypress-mulching operation, and human residences. Large trucks carrying sand and liquid cattle feed frequently passed within 200 to 300 m of many nests. Between the 1988 and 1989 nesting seasons, sand mining moved to within 400 m of one marsh where three pairs of cranes continued to nest.

Five of 11 nests within 400 m of a sand mine, an interstate highway, and a railroad were successful. In 1988, one successful nest was only 55 m from I-4. Five pairs of cranes abandoned their nests in marshes less than 370 m from I-4 after major rains in 1988. Up to 120 cranes roosted in the settling basin of a sand mine which was regularly active at night.

Of the 14 nests not visited during incubation, eight hatched, yielding an apparent success rate of 57%. Apparent success rate for visited nests was 73% of 41 nests. Similarly, Mayfield success estimates were 41% for undisturbed nests and 64% for visited nests.

DISCUSSION

Nest distribution and chronology.—The Green Swamp study area supported a relatively large population of Florida Sandhill Cranes, and aerial surveying appeared to be an efficient method for detecting nests (2.5 nests/h) in the swampy habitat. The 1989 surveys, however, were possibly less comprehensive: more nests may have been missed during the seven fixed-

wing flights due to the higher speed and altitude (Bishop 1988), and also because of the greater time, up to 16 days, between flights. Yet, we were more familiar with the nesting areas during the second year, so we believe the probability of detecting nests was similar for the two years.

Cranes in the Green Swamp nested earlier than those in the Okefenokee Swamp, Georgia (Bennett and Bennett 1990) and Paynes Prairie, Florida (Nesbitt 1988), but later than those on the Kissimmee Prairie, Florida (Walkinshaw 1976). In general, pairs nesting in smaller marshes, which were used less by migrant Greater Sandhill Cranes, began nesting earlier than pairs residing in the larger (>50 ha) marshes which supported more migrant activity. Perhaps resident pairs in these larger marshes spent more time in territorial defense and other social activities involving the migrant subspecies and thus delayed nesting (Nesbitt, pers. comm.).

Hatching success.—Both the Mayfield estimate of 58.8% success and the apparent nest success of 68% are intermediate among those reported for other populations of Florida Sandhill Cranes (Table 3). In general, values from the traditional (i.e., non-Mayfield) method are reported to consistently overestimate success compared to the Mayfield estimates (Hensler and Nichols 1981). Apparent success rates reported in most crane studies are probably biased because a nest can begin and terminate between surveys or searches, resulting in uncounted failed nests. Using radiotelemetered adult cranes, Nesbitt (1988) detected nest initiations earlier and found frequent abandonment soon after initiation in first-time nesters. Thus, his estimates of success probably were less biased.

Predators seem to affect Florida Sandhill Crane nesting less in the Green Swamp than in the Okefenokee Swamp where predators accounted for 75% of all nest failures (Bennett and Bennett 1990). Predation may have been higher in 1989 because of lower water depths in the Green Swamp, permitting greater access to nests in that year. Overall, predation, egg death or infertility, and flooding seemed equally important as sources of nest failure in this study.

Disturbances of any kind that result in an unattended nest can be implicated in such failures as abandonment, predation, and cracked and addled eggs. Although we were unable to determine when an embryo died, it may have been the result of the adult's absence following a nest visit. We were, nonetheless, implicated in at least three nest failures.

Chick recruitment.—Nest success is only one component of reproductive success and has little meaning without assessing other reproductive parameters. Flock counts at a local roost did not necessarily represent the reproductive success of the monitored population but served as an index. Recruitment rates based on flock counts may underestimate productivity because they include nonbreeding subadults and not families that remain

TABLE 3
HATCHING SUCCESS RATES OF FLORIDA SANDHILL CRANE NESTS

Success	N	Location	Reference
39%	53	Paynes Prairie State Park, Florida	Nesbitt 1988
57%	187	Okefenokee Swamp National Wildlife Refuge, Georgia	Bennett and Bennett 1990
68%	102	Green Swamp, Florida	This study
77%	119	Kissimmee Prairie, Florida	Walkinshaw 1982
88%	25	Loxahatchee National Wildlife Refuge, Florida	Thompson 1970

on their territories, which are less gregarious and often do not roost communally (Bishop 1988). In contrast, monitoring only families may overestimate recruitment (e.g., Layne 1983, Bishop and Collopy 1987).

A stable breeding population of Sandhill Cranes requires a recruitment rate of 10 to 12% (Lovvorn and Kirkpatrick 1982). Low hatching success and even lower recruitment rates (5%) in both years of this study indicated that the local population was relatively unproductive and may be declining. In addition, water levels during 1988 and 1989 seemed favorable relative to drier years, as well as to years with more than one rapid rise in water level. Productivity may be substantially lower or absent in less favorable years. Waskinshaw (1976), Layne (1983), Bishop and Collopy (1987), and Bennett and Bennett (1990) reported recruitment rates of Florida Sandhill Cranes ranging from 6 to 57%.

Renesting.—Renesting by Sandhill Crane pairs following the loss of eggs or chicks has been documented for several populations but seems to occur most frequently in southern latitudes, possibly because the nesting season is substantially longer. Bishop (1988) used a 35% (Nesbitt, pers. comm.) proportion to correct/justify the numbers of nesting pairs from her aerial transect sampling to account for the influence of renesting. The incidence of re-nests in the Green Swamp seemed low at 21% but was based on circumstantial evidence since individuals were not marked.

Human disturbance factors.—Cranes that nested near I-4 apparently have acclimated to the continuous traffic noise, but how the highway's proximity affected nesting success remains unknown, especially in the long term. The highway may cause adjacent marshes to flood more rapidly. Proximity to an interstate highway seemed to increase chances of flooding through damming of runoff and drainage from impermeable surfaces. All of the five flooded nests were in marshes less than 370 m from I-4. Otherwise, no trends were found relating nest failures to proximity to

human disturbance or investigator visits, but several possible cases of human-induced nest failures were documented. Walkinshaw (1976, 1981), Valentine (1982), and Stern et al. (1987) discuss the ability of Sandhill Cranes to reside near human disturbance.

In conclusion, we recommend the following steps to be taken to ensure the survival of the threatened Florida Sandhill Crane: (1) researchers should use the Mayfield method for calculating nest success of sandhill cranes if periodic surveys or searching are employed, and visit nests during cool weather and avoid visiting nests during the laying period, (2) agencies should prohibit the construction of impermeable surfaces near wetlands used by nesting cranes to reduce the chances of flooding, (3) require the increased use of culverts in roads that pass through wetland areas, and (4) require buffer zones adjacent to nest marshes to minimize human disturbance and increase potential brood rearing habitat.

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THE ENDEMIC LAND BIRDS OF HENDERSON ISLAND, SOUTHEASTERN POLYNESIA: NOTES ON NATURAL HISTORY AND CONSERVATION

GARY R. GRAVES[1]

ABSTRACT.—New data are presented on the foraging ecology, behavior, vocalizations, body masses, and soft part colors of the endemic land birds of Henderson Island (128°20′W, 24°20′S), southeastern Polynesia. Population estimates of species range from 720–1820 for Stephen's Lorikeet (*Vini stepheni*), 3240 ± for Henderson Island Crake (*Porzana atra*), 3420 ± for Henderson Island Fruit-Dove (*Ptilonopus insularis*), to 10,800 ± for Henderson Island Reed-Warbler (*Acrocephalus taiti*). Conservation issues and translocation of species are discussed. *Received 12 April 1991, accepted 5 Aug. 1991.*

Henderson Island (128°20′W, 24°20′S; Fig. 1), a small elevated coral atoll in the Pitcairn Island group some 2300 km southeast of Tahiti, was colonized and abandoned by Polynesians before it was discovered by Europeans in 1606 (Sinoto 1983, Fosberg et al. 1983). Henderson's four species of endemic landbirds, Henderson Island Crake (*Porzana atra*), Henderson Island Fruit-Dove (*Ptilonopus insularis*), Stephen's Lorikeet (*Vini stepheni*), and Henderson Island Reed-Warbler (*Acrocephalus taiti*), were discovered early this century by phosphate prospectors and described from a few specimens by North (1908) and Ogilvie-Grant (1913). Recent archaeological excavations revealed that at least three additional species of pigeons (*Gallicolumba* sp., two *Ducula* sp.) became extinct during the Polynesian occupation of the island (Steadman and Olson 1985, Steadman 1989). Virtually all that is known about the natural history of the surviving species is contained in the unpublished field notes of Ernest H. Quayle, who collected landbirds on Henderson Island, 12–20 March and 1–13 April 1922, for the Whitney South Seas Expedition of the American Museum of Natural History. Quayle's notes have been liberally paraphrased by Bourne and David (1983).

During 12–22 May 1987, I made natural history observations, conducted censuses, and collected specimens of the landbirds on Henderson Island. The purpose of this paper is to present (1) new natural history observations, (2) population estimates, (3) preliminary descriptions of vocalizations, and (4) specimen data for the endemic land birds. Finally, I discuss the conservation of Henderson's avifauna.

[1] Dept. of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

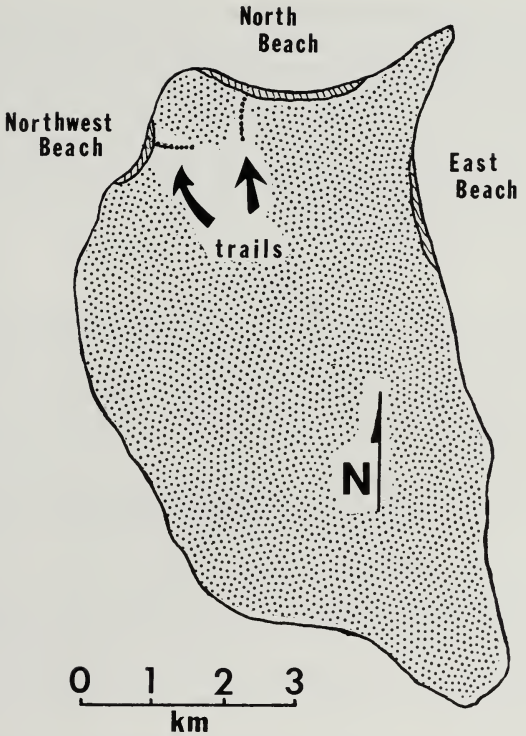

FIG. 1. Henderson Island, southeastern Polynesia, is completely forested. The border of the former ancient lagoon, which begins 400–600 m inland on the north end of the island, has not been mapped. Width of beaches is exaggerated.

HENDERSON ISLAND

Detailed accounts of the physiography, vegetation, and scientific history of Henderson Island are given by Fosberg et al. (1983), Spencer and Paulay (1989), and Paulay and Spencer (1989), from which the following description is partly derived. Henderson Island is an ancient coral reef and lagoon that has been thrust 30 m above sea level by lithospheric flexure under the weight of Pitcairn Island (200 km WSW of Henderson). Henderson Island, which appears flat-topped from a distance, has maximum dimensions of 9.6 × 5.1 km and an area of 36 km^2. Its shoreline is characterized by vertical cliffs (15–30 m) interrupted by three narrow beaches (Northwest, North, and East) on the northern end of the island. Wave action is unusually intense and landings are treacherous. From high vantage points along the northwest coast, surf spray may be seen through binoculars on the south side of the island some 7–8 km away. The entire island appears to be heavily forested. With the exception of introduced coconut palms (*Cocos nucifera*) and four other adventive species along the beaches, the vegetation of Henderson Island is undisturbed; miro (*Thespesia populnea*) and sandalwood (*Santalum hendersonense*) are occasionally harvested by Pitcairners. Away from cliff edges,

the interior of the island is covered with a low (4–9 m), tangled, nearly impenetrable forest. Except in the central area formerly occupied by a lagoon, passage is hampered by exceptionally rough terrain of jagged limestone pinnacles, fossil coral rubble, and small sink holes. Understory vegetation may be lush in well-lit exposures, but a thick layer of leaf litter is found in taller forest with a closed canopy. Permanent sources of fresh water in the island's interior are unknown. Dominant trees on Henderson include *Cocos nucifera, Pandanus tectorius, Thespesia populnea, Tournefortia argentea, Cordia subcordata, Guettarda speciosa, Pisonia grandis, Geniostoma hendersonense, Nesoluma st-johnianum, Hernandia stokesii, Myrsine hosakae,* and *Celtis* sp.

METHODS

Most observations were made in the narrow strip of forest behind Northwest Beach (700 × 30 m = 2.1 ha) and along an 875 m trail into the island's interior, cut roughly perpendicular to the shoreline (Fig. 1). Censuses along the beach (N = 8 days; 10.75 h) and trail (N = 6 days; 19.75 h) were made by walking slowly and mapping all birds seen or heard in relation to trail markers. Because the few species present were tame and responded readily to "squeaks" and tape playbacks of their vocalizations, the location of nearly all individuals along the census route was determined. Detection distances for vocalizations of each species were estimated from repeated observations in beach front forest and in the island's interior away from surf noise.

A narrow strip of forest behind North Beach (750 × 35 m = 2.63 ha; 3.5 h) and a previously cut trail (ca 1 km; 1.5 h) perpendicular to North Beach were censused by the same methods on 20 May. North Beach censuses are less reliable because of their short duration.

Vocalizations were recorded with a Sony TCM-5000 cassette recorder and condenser microphone and analyzed on a Uniscan II real-time spectral display analyzer (Multigon Industries).

Stomach contents of specimens collected for genetic and anatomical studies were preserved in alcohol. Body masses of males and females were compared with two-tailed *t*-tests. All specimens are deposited in the National Museum of Natural History, Smithsonian Institution.

SPECIES ACCOUNTS

Henderson Island Crake.—This is the last surviving species of flightless rail in Polynesia (see Steadman 1989). It was common in the interior of the island and along the bases of cliffs above the beaches. This small black-plumaged crake is rather tame and inquisitive, approaching stationary observers to within 2 m. Its preferred habitat is shady understory of low dense forest carpeted with a thick layer of leaf litter. Foraging birds obtained food items, most too small to identify through binoculars, by scratching and flicking aside leaves with their feet and bill. Stomachs (N = 2) contained small land snails and insect parts.

Pairs of crakes often foraged together, usually within 10 m of one another, and maintained contact with a frog-like callnote, "kwa." Rapid series of similar notes were given by agitated crakes in response to playback of vocalizations (Fig. 2). Birds were especially vocal in early morning

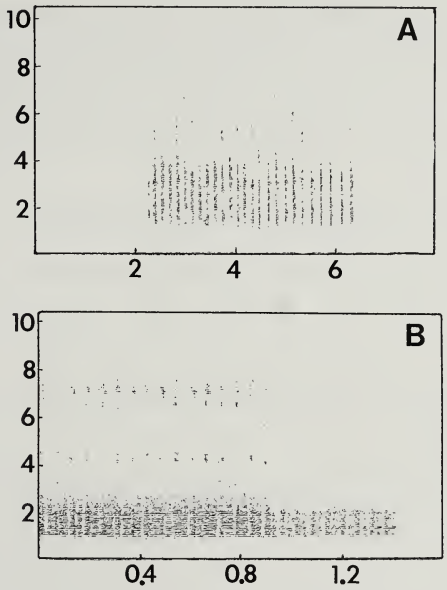

FIG. 2. Spectrograms of vocalizations of the Henderson Island Crake (*Porzana atra*). A: rapid callnotes given by crake in response to playback. B: terminal portion of duet where one crake of pair ceased calling. X-axis of all sonagrams in seconds; Y-axis in kHz.

and at dusk. Twice I observed duetting displays of pairs. In each instance one crake began calling and running rapidly, with slightly raised wings and lowered head, through the undergrowth to its presumed mate. The pair commenced duetting (3.7–4.1 sec) as soon as they were in physical contact. Pairs often engaged in bouts (0.25–2.0 min) of allopreening after the duetting ceased. On a third occasion, I observed a pair of foraging adults followed by a full-sized subadult; when the adults began duetting, the subadult joined them, and all three called simultaneously.

Population estimates were based on sight and vocal records. In the island interior away from the surf, crake vocalizations could be heard from a distance of 75 m. However, within 300 m of the beach, I had difficulty hearing vocalizations more than 50 m away. Therefore, I estimate that I censused a transect with average dimensions of 875 × 133 m along the Northwest Beach and 1000 × 135 m along the North Beach trail. A minimum of six pairs were present along the Northwest Beach trail, two pairs below the cliffs on Northwest Beach, seven pairs along the North Beach trail, and four pairs below the cliffs at North Beach. Based on these data, the density of crakes along the beach fronts, where every

bird could be located, ranged from 0.95 pairs/ha to 1.53 pairs/ha. Assuming home ranges were non-overlapping, completely packed, and randomly sampled, crake densities in the island's interior were estimated to be 0.52 pairs/ha on both transects. Using an arbitrary conservative figure of 0.45 pairs/ha, the total population of *Porzana atra* was estimated to be 3240 ± individuals.

Gonads of collected specimens were not reproductively active. Body masses of males (N = 3, 78–82 g, $\bar{x}$ = 80.3 ± 2.1) and females (N = 6, 76–88 g, $\bar{x}$ = 79.0 ± 4.8), including subadults of both sexes, were statistically indistinguishable (t = 0.45, $P > 0.05$). Sexes cannot be identified under field conditions. Soft parts are vividly colored: iris, red; eyering, orange; feet and legs, reddish-orange; bill, black, base of culmen green. Subadult birds, similar in size to adults, were identified by dusky tarsi and dark orbital skin.

Henderson Island Fruit-Dove.—Low-pitched advertising calls of *P. insularis* were a conspicuous feature of the interior forest on Henderson (Fig. 3). Fruit-doves were fairly tame and approached observers to within 3 m in response to "squeaking." They frequently flew over the forest canopy for 100–200 m but appeared to be territorial and responded to playbacks of their calls. Most calling was done from the vicinity of fruiting trees. Although cooing notes may be given occasionally by females, I assumed that series of calls were given by males. Cooing fruit-doves could be detected from a distance of about 75 m in the island interior and 50 m within 300 m of the surf. I found a minimum of 12 doves along the Northwest Beach trail, six below the cliffs at Northwest Beach, 10 along the North Beach trail, and six below the cliffs of North Beach. Densities of individuals varied from 2.29 to 2.86 doves/ha along beach fronts and from 0.74 to 1.03 doves/ha in the island's interior. Because fruit-dove censuses along the Northwest Beach trail were repeated on six different days, I believe the density estimate from this location was the most accurate. Using an arbitrary conservative figure of 0.95 fruit-doves/ha, the total population of *Ptilonopus insularis* was estimated to be 3420 ± individuals.

Specimens had moderately enlarged gonads (i.e., thickened oviducts and enlarged testes). Stomachs (N = 3) contained fruit pulp and intact fruits (*Nesoluma st-johnianum, Ixora fragrans,* and another unidentified species). Soft part colors of sexes were similar: iris, orange becoming yellower near pupil; bill, greenish-yellow becoming yellower at base; orbital skin, bluish-gray; eyering, pale yellow; legs and feet, coral red; toe pads, pale yellow. Juveniles lack the purplish-crimson crown of adults. Body masses ranged from 102–105 g in males (N = 2) and from 95–105 g in females (N = 3).

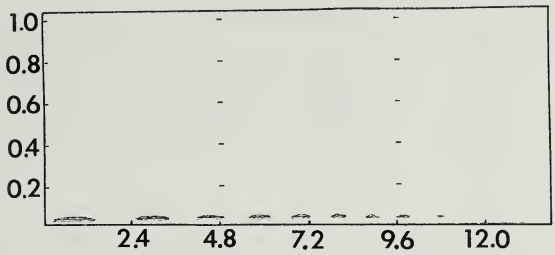

FIG. 3. Spectrograms of advertising song of Henderson Island Fruit-Dove (*Ptilonopus insularis*).

Stephen's Lorikeet.—Stephen's Lorikeets were a conspicuous feature of our encampment on Northwest Beach where they fed on coconut (*Cocos nucifera*) nectar. They were seen frequently in small flocks of 3–5 (possibly family groups) flying 20–40 m over the forest canopy. Despite their brilliant red, green, and yellow plumage, they were difficult to locate once they alighted in foliage. Feeding birds were often detected by their soft twittering calls. Flight calls were louder and could be detected at a distance of 100 m, away from the surf (Fig. 4). Because lorikeets made relatively large daily movements, I estimated their local abundance by recording the number of lorikeets observed along the beach and interior forest trails during a continuous census, taking into account the location of flocks and the destination of flying birds. Single census maxima of 14 and 11 individuals were observed, respectively, at Northwest Beach and North Beach. Estimates of total population size were difficult to make because coconut groves along the beach attract lorikeets from the island's interior. However, I speculate that lorikeet density falls between 0.2 and 0.5 individuals/ha, a total population size of 720 to 1820 individuals.

Of five specimens collected, one female had a greatly enlarged ovary and thickened oviduct, but the others had quiescent gonads. Body masses varied from 42–51 g for females (N = 4) to 55 g for a single male. Subcutaneous fat was moderate to heavy. Soft part colors of *V. stepheni* reported by Ogilvie-Grant (1913) were based on faded specimens. Colors of freshly collected specimens were as follows: iris, pale to medium orange; feet and legs, orange; bill, orange with dusky markings at tip of upper mandible.

Henderson Island Reed-Warbler.—This abundant reed-warbler occurs throughout the island, and possibly outnumbers the combined populations of the other three endemic species. Typically, pairs of adults were accompanied by one or two fully grown subadults. Warblers foraged on all substrates (i.e., foliage, twigs, branches, bark crevices, etc.) from ground

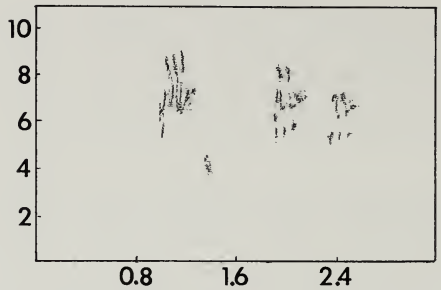

FIG. 4. Spectrograms of flight calls of Stephen's Lorikeet (*Vini stepheni*).

level to the upper fronds of the tallest coconut palms. Field observations, supplemented by stomach contents, showed that Henderson Island Reed-Warblers have catholic diets that include several species of land snails (1–3 mm), ants, flies, beetles, cockroaches, large wasps, seeds, and fruit pulp.

The closely related Pitcairn Reed-Warbler (*Acrocephalus vaughani*), of Pitcairn Island, rarely forages near ground level and is much warier than *A. taiti* of Henderson. This behavioral difference may be related to the presence of cats and humans on Pitcairn. Henderson Island Reed-Warblers (*Acrocephalus taiti*), as well as reed-warblers from Pitcairn Island and Rimitara (*A. rimitarae*) in the Austral Islands, were reported by Holyoak (1978) to give a variety of chirping calls but no song. Holyoak's data on Henderson Island Reed-Warblers were taken from Quayle's field notes. My observations suggest that the lack of song may be a matter of interpretation. Most vocalizations of *A. taiti* are high pitched (4–8 kHz) single notes of short duration (<0.13 sec). However, series of thin, longer notes (1–5 sec) given by adult territorial birds, albeit in an unknown context, resemble song (Fig. 5). These vocalizations can be clearly heard at 25 m above the white noise of wind and surf (both predominately 0–3 kHz) along the beaches, and probably function in interterritorial communication, given the small territory size of *A. taiti.*

Henderson Island Reed-Warblers apparently breed during the austral summer and none of the specimens collected was in breeding condition. One family group, consisting of an adult pair and a warbler in subadult plumage that begged for food, attended a recently built nest and occasionally added nesting material. On several days, I observed an adult sitting on the nest, as though incubating. However, periodic checks of the nest with a mirror between 12 and 20 May revealed no eggs. A brief

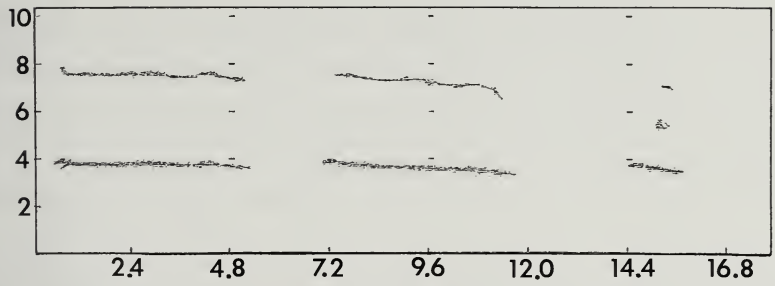

FIG. 5. Spectrograms of vocalizations, possibly song, of Henderson Island Reed-Warbler (*Acrocephalus taiti*).

account of the previously undescribed nest of *A. taiti* follows. The nest was built in a fork of a thin and nearly horizontal lower branch of *Thespesia argentea,* 4 m above ground level, in the lower canopy of relatively tall forest (7 m) below the cliffs of North Beach. The bulky nest was composed of thin rootlets and *Cocos* fibers and lined with finer material. Outside dimensions were 210 × 200 mm wide and 80 mm deep; the nest cup was 55 mm in diameter and 45 mm deep. A second weathered nest found nearby was constructed with similar materials.

Holyoak (1978) speculated that the conspicuous plumage leucism of *Acrocephalus* from Rimitara, Pitcairn, and Henderson islands was somehow correlated with the loss of song. The pattern of leucism is strikingly different among these taxa (Graves, in prep.), affecting primarily the anterior body plumage, secondaries, and rectrices of *A. taiti,* the primaries, secondaries, and rectrices of *A. vaughani,* and scattered parts of the plumage of *A. rimitarae.* In all three taxa, leucism appears to progress with age in both sexes. Specimens of *A. taiti* (N = 7) with crania less than 75% pneumatized lack leucistic feathers. Holyoak (1978) suggested that the occurrence of leucism may allow individuals to recognize each other and facilitate territorial defense. Although leucistic reed-warbler plumage may function as a signal in dominance hierarchies, plumage patterns are unstable and may change at every molt for several years before converging in the "typical" Henderson Island pattern. This argues against behavioral selection of plumage pattern for individual recognition. In any event, there is no evidence that leucism is a consequence of songlessness or vice versa.

Fundamental differences in the sequence and pattern of leucistic plumages among the reed-warblers of Rimatara, Pitcairn, and Henderson suggest substantial genetic differentiation at the species level. This idea is

supported by differences in subadult plumages and the color of mouth-linings on Pitcairn (orange) and Henderson (pinkish-orange or "peach"). Because populations of reed-warblers on all three islands are relatively small and separated by great distances of open ocean, gene flow among islands is probably infinitesimal. Lumping the three taxa on the basis of superficial appearance (Murphy and Mathews 1929) is clearly unwarranted. Until contradictory information becomes available, I consider the three populations of "leucistic" reed-warblers as separate species.

Reed-warbler populations were censused by vocalizations, sight records, and selective collecting. Chipping notes and song-like phrases could be heard up to 50 m away under windless conditions inland and about 30 m away within 50 m of the surf. Territories were small, and available habitat appeared to be saturated. A minimum of 10 reed-warblers (including subadults) occurred along Northwest Beach, 25 along the Northwest Beach trail, 27 along North Beach, and 12 (thought to be an underestimate) along North Beach trail. Estimated densities varied from 1.36 reed-warblers/ha on the North Beach trail to 10.29 reed-warblers/ha along North Beach. I believe censuses along the Northwest Beach trail (3.31 reed-warblers/ha) more accurately reflect reed-warbler densities in the island's interior. Using an arbitrary conservative estimate of 3.0 reed-warblers/ha, I estimated that the total population of Henderson Island Reed-Warblers was 10,800 ±.

Soft parts of warbler specimens were as follows: iris, brown; feet and legs, medium gray; upper mandible, dark grayish-brown; lower mandible, silvery-flesh with a dusky tip. Subcutaneous fat was moderate to heavy. Body masses of males (N = 21, 22.5–30.5 g, $\bar{x}$ = 25.8 ± 2.0) were significantly greater than those of females (N = 19, 21.0–25.0 g, $\bar{x}$ = 22.8 ± 1.11) (t = 5.89, $P < 0.0001$).

CONSERVATION

The accumulating knowledge of prehistoric avifaunas in southeastern Polynesia (reviewed in Steadman 1989) indicates that most, if not all, flighted species were more widespread in the past, and most flightless species are extinct. These data have important implications for conservation strategies. For instance, Henderson once supported as many as four species of pigeons ranging in size from the surviving fruit dove (105 g) to two large species of *Ducula* with estimated body masses of 400 g and 800 g, respectively (see Steadman and Olson 1985). Historically, the nearest occurrences of *Ducula* pigeons to Henderson Island have been in the Society and Marquesas islands more than 2000 km distant. Strong-

flying pigeons as well as the Stephen's Lorikeet (*Vini stepheni*) probably occurred on Pitcairn Island as well, although fossil evidence of their residency has not yet been discovered. In other words, avifaunas throughout Polynesia have been drastically altered by man and may now bear little resemblance to their primeval condition. It is probable that nearly every vegetated island in southeastern Polynesia the size of Henderson or larger once supported a flightless rail, one or more pigeons, a lorikeet, and a reed-warbler.

Current predation on the eggs, nestlings, and adults of Henderson's land birds is probably limited to the Pacific rat (*Rattus exulans*), introduced by the Polynesians, and a large terrestrial hermit crab. Crabs are ubiquitous nocturnal scavengers in beach front forest but were uncommon in the island's elevated interior. *Rattus exulans,* however, occurred commonly in all habitats and was observed in the upper branches of trees. The surviving land birds on Henderson Island apparently have adapted to the presence of *R. exulans,* or at least are able to co-exist with it. Present levels of wood-cutting by Pitcairners pose little threat to the island's avifauna, while the introduction of the coconut palm may actually have benefited the Stephen's Lorikeet.

The greatest potential danger for Henderson's birds is the possible introduction of other mammalian predators, especially the black rat (*R. rattus*) (see Atkinson 1985). Release of domestic cats or a second species of rat by visiting yachts or disabled ships would probably cause the rapid extinction of Henderson's crake and perhaps other species (Greenway 1958, Ripley 1977, Atkinson 1985). Undisputable evidence (e.g., rubbish, charcoal) of past landings was seen on both Northwest and North Beach areas. The introduction of mosquitoes and avian malaria is perhaps less of a threat because of the lack of fresh water on Henderson. Mosquito ovipositing sites would be restricted to small temporary pools of rainwater on karst surfaces and in sparsely distributed tree holes. Mosquitos were abundant on nearby Pitcairn (*Aedes aegypti, Culex quinquefasciatus*: Mathis 1989) which has permanent sources of fresh water. The latter species is a vector of avian malaria in Hawaii (Warner 1968, van Riper et al. 1986). Another potentially devastating disease for which Henderson's endemic birds may have no immunity is avian pox (see Warner 1968). Unfortunately, avian pox is transmitted by hippoboscid and other biting flies, which are already present on Henderson, as well as by mosquitoes.

Available data indicate that land bird populations on Henderson Island are relatively stable. Yet, despite the island's great isolation, accidental introduction of predators, disease vectors, and diseases is probably inevitable because of unauthorized landings of yachts. Clearly, other con-

servation measures should be considered in addition to legislating the inviolability of Henderson's biota.

One potential conservation tool is the establishment of populations of Henderson's endemic land birds on "bird-less" islands in southeastern Polynesia. Establishment of viable populations on the islands would be an important hedge against extinction in the event of catastrophic mortality on Henderson. Unfortunately, translocation is often a strategy of last resort in conservation biology. In fact, Diamond (1985) suggested that translocation be used only for those species for which there is no realistic hope of survival in the wild on their native islands. However, translocation efforts are much more successful when larger numbers of individuals are transplanted (Griffith et al. 1989). Ironically, by the time a species is recognized as threatened or endangered, populations are often so small that translocation efforts have a low probability of success. Thus, translocation or captive propagation of Henderson's endemic species as well as many other Polynesian endemics should be implemented in the near future while populations are still high. Why wait for another Guam-like faunal debacle?

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ISLAND EXTINCTIONS: THE CASE OF THE ENDANGERED NIGHTINGALE REED-WARBLER

James D. Reichel,[1] Gary J. Wiles,[2] and Phil O. Glass[1]

Abstract.—Current status of Nightingale Reed-Warblers (*Acrocephalus luscinia*) in the Mariana Islands was examined by field surveys and responses to tape recordings of calls. Historic status was determined using the literature, museum specimens, and field notes of previous researchers. Reed-warblers, historically found on five of the Mariana Islands, currently are thought to be extinct on Guam, Aguijan, and Pagan. Substantial numbers still remain on Saipan and Alamagan. Reasons for extinctions may include loss of wetlands and understory vegetation by volcanic activity, land development, and feral ungulates; fires in wetlands; pesticides; and predation by brown tree snakes (*Boiga irregularis*). *Received 25 Feb. 1991, accepted 1 July 1991.*

During the past 400 years, bird extinctions rarely have occurred in continental areas; of the 217 species or races that have disappeared, all but 17 are insular forms (Halliday 1978). In the Hawaiian Islands alone, more bird species are threatened or endangered than in the entire continental United States (USFWS 1987). Sixteen of twenty native land and freshwater bird species in the Mariana Islands are listed by federal or local governments as threatened or endangered on at least one island. The 15 Mariana Islands form an 812-km long, north–south oriented archipelago, with a total land area of 1018 km^2 (Fig. 1). All are high tropical islands, and several are still actively volcanic.

The Nightingale Reed-Warbler (*Acrocephalus luscinia*) is listed as federally endangered in the Mariana Islands by the U.S. Fish and Wildlife Service (USFWS 1970). The specific and subspecific taxonomic designations of the Nightingale Reed-Warbler have varied among researchers. Some authors have included populations from the Mariana Islands, Caroline Islands, and Nauru within *A. luscinia* (Baker 1951, Mayr 1978). Others considered the species restricted to the Marianas (Oustalet 1896, Pratt et al. 1987) or, most commonly since 1940, to both the Marianas and Carolines (Yamashina 1942, Pyle and Engbring 1985). For the purposes of this paper, we consider *A. luscinia* to be endemic to the Mariana Islands. Subspecific designations also remain in question. All recent authors consider the Pagan (*A. l. yamashinae*) and Aguijan (*A. l. nijoi*) populations to be single-island endemics. Yamashina (1942) considered the Guam population to be endemic (*A. l. luscinia*) and the other popu-

[1] Division of Fish and Wildlife, Saipan, MP 96950. (Present address JDR: Wildlife Resource Management Program, Yakima Indian Nation, P.O. Box 151, Toppenish, Washington 98948. Present address POG: U.S. Fish and Wildlife Service, 17629 El Camino Real, Houston, Texas 77058.)
[2] Guam Division of Aquatic and Wildlife Resources, P.O. Box 2950, Agana, Guam 96910.

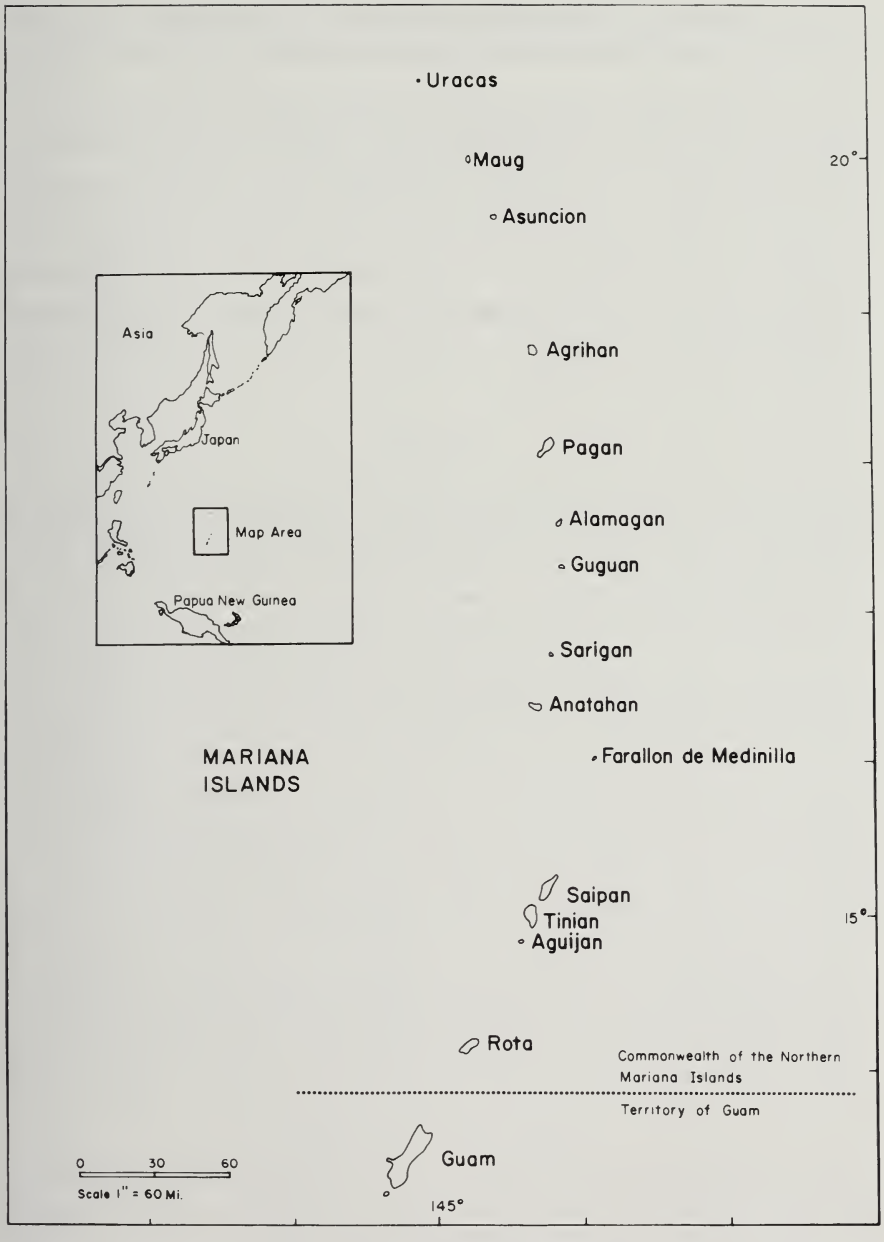

FIG. 1. Map of the Mariana Islands.

lations (Saipan and Alamagan) to belong to *A. l. hawae*; Baker (1951) felt populations from Guam, Saipan, and Alamagan should all be considered *A. l. luscinia.*

Bird surveys of the southern islands were conducted on Guam in 1981 (Engbring and Ramsey 1984) and Saipan, Tinian, Aguijan, and Rota in 1982 (Engbring et al. 1986). The Nightingale Reed-Warbler was extinct by 1981 on Guam, while it was found to be common on Saipan and rare on Aguijan. Pagan and Alamagan populations were known only from specimens collected prior to 1945; no estimates of population sizes were available. In this paper we examine the current status and historical changes in Nightingale Reed-Warbler populations on each island and relate these changes to habitat availability and usage.

METHODS

To determine historical populations of this species we (1) examined accounts in the literature; (2) wrote museums for lists of specimens; and (3) examined field notes of previous researchers in the Marianas, including those in the Guam Division of Aquatic and Wildlife Resources (GDAWR) and Commonwealth of the Northern Mariana Islands Division of Fish and Wildlife (CNMI-DFW). POG and JDR spent three years working on Saipan for the CNMI-DFW, while GJW spent seven years working on Guam for the GDAWR. Current status on other islands was evaluated by surveys conducted on Aguijan (12 trips, 75 man-days), Alamagan (one trip, nine man-days), and Pagan (six trips, 29 man-days). These surveys included audio tape play-back to locate birds and to determine territorial boundaries, and simple watching/listening for birds by biologists familiar with, and looking/listening for, reed-warblers. On Aguijan, calls were played at least once since 1986 over the entire island (720 ha), at distances no more than 300 m apart, and additional times in areas where reed-warblers were observed from 1981–1985. On Alamagan (1130 ha), calls were played at 20–40-m intervals for 2 km up a major gully to determine approximate territory boundaries and size. The territory size was extrapolated to similar habitat throughout the island to estimate the number of pairs present. The remainder of the island was traversed in conjunction with other wildlife surveys. On Pagan (4830 ha), we played tapes at 100-m intervals over both wetland areas; additionally, about a third of the non-wetland area was surveyed with tape-playbacks performed at 300-m intervals. Approximately two-thirds of the island was covered one or more times during general wildlife surveys by people who were familiar with reed-warbler vocalizations. All Mariana Islands (except Medinilla) where reed-warblers were not historically known were visited at least three times during 1978–1989; no reed-warblers were found and no additional information on these islands is presented.

RESULTS AND DISCUSSION

Guam.—Historic accounts indicate that Nightingale Reed-Warblers were generally restricted to freshwater and brackish wetlands and river basins located on the west-central side of the island. Birds are known to have occurred at the Agana Swamp, the Atantano River marsh in Santa Rita, a low lying area near the mouth of the Masso River in Piti, and an undescribed site in Agat (Safford 1905, Bryan 1936, Stophlet 1946, Baker

1948, 1951, Kibler 1950, GDAWR, unpubl. data). A. Marche also collected birds from a presently unknown site called Snajahan (Oustalet 1895).

Reed-warblers inhabited thick cane stands and adjacent shrubbery and small trees at these localities (Seale 1901, Safford 1905, Stophlet 1946, Kibler 1950, Baker 1951, GDAWR, unpubl. data). The type of cane referred to by many authors was probably *Phragmites karka,* a tall reed that has predominated at many of Guam's wetlands for at least the last century (Safford 1905, Fosberg 1960). Reed-warblers were also known to have occurred in groves of the small introduced tree, tangantangan (*Leucaena leucocephala*) (Hartin 1961); King (1962) observed birds on a brushy hillside far from any wetland.

The type specimen of *A. luscinia* was collected by Quoy and Gaimard (1830 in Baker 1951) during their visit to Guam in 1828. Subsequent observers provided conflicting assessments of reed-warbler abundance, perhaps because of the species' limited distribution and secretive habits (Baker 1951). They were described as rare or scarce by Seale (1901), Bryan (1936), Stophlet (1946), Kibler (1950), and Mayr (1945). However, Safford (1902) claimed that they were "not rare" in the Agana Swamp. Baker (1951) and his collecting team also found *A. luscinia* to be fairly common at some locations, particularly in the Agana Swamp.

In 1960, Hartin (1961) reported Nightingale Reed-Warblers to be fairly common, and King (1962) saw several during a three-day visit to the island. A few reed-warblers remained in the Atantano River marsh until early 1968 (J. Jeffrey, pers. comm.). The birds were still fairly common in parts of the Agana Swamp in 1967 or 1968 (J. Jeffrey, pers. comm.) but then rapidly disappeared. The last known sighting of a reed-warbler on Guam occurred there in 1969 (GDAWR, unpubl. data). Numerous searches of all Guam wetlands since 1970 have not detected reed-warblers (Pratt et al. 1979; Ralph and Sakai 1979; Tenorio and Associates 1979; Jenkins 1983; Engbring and Ramsey 1984; GDAWR, unpubl. data).

The reed-warbler's limited habitat distribution probably made it vulnerable to disturbances of wetlands. Rice and taro were grown in several of the island's wetlands from the 1800s until World War II (Seale 1901, Safford 1905, Thompson 1947, Baker 1951). These agricultural activities resulted in the draining and cutting of sizable areas of reed beds and probably reduced reed-warbler numbers (Seale 1901). Wetland cultivation of crops declined after World War II, allowing a resurgence of natural marsh vegetation at many locations (Baker 1951, Solenberger 1967).

There is little evidence that habitat loss caused the final decline of reed-warblers on Guam (GDAWR, unpubl. data), despite recent suggestions (Jenkins 1983, Engbring and Ramsey 1984). Some filling of wetlands

occurred in the 1960s and 1970s, especially in the Agana Swamp, but luxuriant stands of *Phragmites,* ranging from 1–70 ha, continue to persist on the island to the present (Stinson et al. 1991).

Baker (1951) believed that dry season marsh fires were potentially harmful to Nightingale Reed-Warblers at some sites. Several fires burned through large portions of the Agana Swamp in the 1960s (G. S. A. Perez, pers. comm.) and may have adversely affected reed-warbler numbers in the marsh.

Drahos (unpubl. data) contended that pesticide use was a more likely cause of the reed-warbler decline but had no direct evidence of this. After World War II, DDT was applied liberally for insect control on Guam, Saipan, and Micronesian islands occupied by the military (Baker 1946). The U.S. Navy also conducted a spraying program on Guam in the late 1950s and 1960s to combat the threat of mosquito-borne diseases such as malaria and dengue (GDAWR, unpubl. data). It is likely that wetlands were targeted in these control programs in an effort to reduce mosquito numbers. Tests conducted in 1981 indicated that pesticide levels on Guam were low and probably not responsible for the current declines of Guam forest birds (Grue 1985). However, pesticides cannot be ruled out as a cause for the earlier reed-warbler extinction.

We speculate here that predation by brown tree snakes (*Boiga irregularis*) may have played a key role in the final disappearance of Nightingale Reed-Warblers on Guam, as it did in the extinction of native bird species in forest habitats on the island (Savidge 1987, Engbring and Fritts 1988). Baker (1951) felt reed-warblers had never been abundant on Guam and that lack of predators, especially snakes, may have allowed them to survive in low numbers through the 1940s. Tree snakes were introduced to Guam after World War II and first appeared in south-central Guam in the 1950s in the vicinity of the U.S. Naval Magazine, which is only 3–5 km from several of the swamps formerly used by reed-warblers. The snake population gradually increased and radiated outward into southern and central Guam by the late 1960s and early 1970s (Savidge 1987). This spread coincides with the decline of reed-warblers. Tree snakes are generally thought to avoid marshes, although there have been rare sightings in this habitat. However, snakes almost certainly forage in shrubs and trees next to reedy wetlands. The reed-warbler's use of shrubby edge vegetation at swamps may have made it more vulnerable to snake predation than biologists have previously believed.

Aguijan.—The only pre-1945 evidence of reed-warblers are five specimens taken by a Japanese collector on 29 February 1940, all currently in the Yamashina Institute for Ornithology (K. Momose and T. Hiraoka, pers. comm.). This small collection indicates that the bird was more

common prior to World War II than by the time of the intensive surveys conducted in the early and mid-1980s. G. D. Peterson (unpubl. data) found Nightingale Reed-Warblers to be one of the least common forest birds in 1954 on Aguijan, while an intensive U.S. Fish and Wildlife Service forest bird survey in 1982 (Engbring et al. 1986) estimated the population at 4–15. A maximum of six birds was recorded on one of the four trips by CNMI-DFW personnel during 1983–1985 (30 man-days), and the last sighting occurred in July 1985 (D. Aldan, pers. comm.). None was found during 1987–1990 on eight trips by JDR, POG and other CNMI-DFW personnel (45 man-days). It seems likely that the endemic subspecies (*A. l. nijoi*) on Aguijan is extinct.

Under the Japanese administration (1914–1945), Aguijan was heavily farmed, resulting in extensive clearing and modification of the vegetation. Goats, feral on the island since at least the early 1950s, have destroyed most of the forest understory, preventing many tree species from regenerating. No wetlands occur on Aguijan; reed-warblers were apparently restricted to native forest areas, particularly those areas with dense canopy cover (Engbring et al. 1986; CNMI-DFW, unpubl. data). The extreme habitat changes during the past several decades, coupled with small island size, were likely responsible for the extinction of the bird on this island.

Saipan.—The Nightingale Reed-Warbler was first reported from Saipan by Hartert (1898). Additional collecting took place under the Japanese administration when collectors obtained 22 specimens during three periods totaling about 60 days in 1931–1932; 10 are currently in the Yamashina Institute (K. Momose and T. Hiraoka, pers. comm.). During the Japanese period, much of the Lake Susupi area and more than 50% of Saipan was used for agriculture (USACOE 1986). Reports immediately following World War II indicate a small population of reed-warblers was present and probably restricted to wetland areas (Stott 1947, Marshall 1949).

More recently we have found Nightingale Reed-Warblers common over much of the island in both wetland and upland habitats. Ralph and Sakai (1979) estimated there were 45/km^2 in a 7.3-h census. This number is similar to the 46/km^2 found in a much more intensive survey of the entire island with 488 eight-min counts in 1982 (Engbring et al. 1986). Much land has been cleared over the past decade, and this development is continuing at an accelerating pace. This will certainly reduce the population in the near future.

Nightingale Reed-Warblers on Saipan currently use a wide variety of habitats ranging from *Phragmites* wetlands to tangantangan stands and native limestone forest (rarely). We have found them most commonly at wetland/upland ecotones and in mixed tangantangan/grassland habitats,

as did R. Craig (pers. comm.). These are both characterized by dense understory. The current population is certainly high compared to that found following World War II and is likely higher than early periods. This may be due to one or more of the following factors: (1) increased edge habitat from fragmentation in recent decades; (2) replacement of large tracts of native forest with tangantangan forest; and/or (3) adaptation of Nightingale Reed-Warblers to new habitat types.

Alamagan.—H. Orii of the Yamashina Institute collected five specimens on 18 February 1931 (K. Momose and T. Hiraoka, pers. comm.), the only record of this species prior to our survey in 1988 (nine man-days). We played taped songs to survey this species on the south side of the island. During intensive surveying up a typical long wooded gully, we found territories at 60–100 m intervals. Birds were seen in habitats with a partially open overstory and somewhat brushy understory; they also were seen in dense swordgrass (*Miscanthus floridulus*), but only within about 50 m of an ecotone. Birds were not seen in the denser forests at elevations over 300 m. Based on the amount of suitable habitat and territory size, we calculated a population of at least 100 pairs on the south side of the island. We did not get to the north side of the island; however, a 1990 survey by other CNMI-DFW personnel confirmed that reed-warblers were also common there (C. Rice, pers. comm.). Our estimate for the Alamagan population is conservatively 350 pairs; actual numbers could range to a maximum of 1000 pairs.

Feral goats, pigs, and cattle have drastically changed the vegetation of Alamagan since their arrival in the mid-1700s (S. Russell, pers. comm.). At lower elevations, the forested gullies have the only remnant native vegetation, primarily trees. The understory is largely composed of introduced species. The ground vegetation (except swordgrass areas) is sparse, reminiscent of desert badlands with open spaces between individual plants (perhaps 50% ground cover). At all elevations, the ridges and most slopes are covered by tall, thick swordgrass. Vegetation and erosional patterns are characteristic of islands with a long history of overgrazing by feral ungulates.

Pagan.—Little information is available on the population of Nightingale Reed-Warblers from Pagan except specimen collections by Marche (10 in 1887) (Marche 1889; Oustalet 1895; C. Jouanin, pers. comm.) and Orii (19 in 1931) (K. Momose and T. Hiraoka, pers. comm.) that indicate it may have been locally common in wetlands. D. Aldan and J. Sablan, two former residents of the island, report the last reed-warblers were present until at least the 1960s but occurred only in the wetlands near the upper, or possibly both, of the island's lakes. Despite intensive searching in the vicinity of both lakes, we (and other CNMI-DFW personnel)

failed to find reed-warblers during six trips to Pagan (29 man-days) in 1983–1989 nor did other researchers in the late 1970s (Tenorio and Associates 1979; R. Clapp, pers. comm.). It seems probable that the endemic subspecies (*A. l. yamashinae*) on Pagan is extinct.

Wetland habitat has been drastically altered and reduced on Pagan during the last century. Major causes include 1914–1945 Japanese development; feral goats, pigs, and cattle; and a 1981 and later volcanic eruptions (Marche 1889, Corwin et al. 1957, Tenorio and Associates 1979). By 1979, there was little shoreline vegetation at either lake (Tenorio and Associates 1979). The 1981 and following eruptions eliminated all herbaceous and most woody vegetation in the upper lake area which is only now (1989) beginning to make a comeback. There is currently less than a 1% vegetative ground cover bordering both lakes and no emergent vegetation in either.

Habitat and extinction.—The Nightingale Reed-Warbler has become extinct on islands where it was primarily restricted to wetlands (Guam and Pagan). This is not surprising, given the fate of the other three wetland bird species native to the Marianas. The Marianas Mallard (*Anas platyrhynchos oustaleti*) and White-browed Crake (*Poliolimnas cinereus*) are both extinct (Jenkins 1983, Reichel and Glass 1991). The Marianas Common Moorhen (*Gallinula chloropus guami*) is endangered throughout the Marianas and extinct on Pagan and Rota (Becker and Butler 1988, Stinson et al. 1991). Vegetated wetland habitat has been essentially eliminated on Pagan, the decline taking place over at least 60 years. Moderate losses have occurred on Guam, but the area lost has never been quantified. Fires and cultivation in wetland areas at times may also have contributed to reed-warbler declines.

On Guam, habitat loss probably did not cause the final decline of the reed-warbler. Brown tree snakes may have played a key role in the final extinction of the reed-warbler, as they have in the declines of other native birds (Savidge 1987, Engbring and Fritts 1988).

The cause of extinction on Aguijan is less clear cut. We agree with Engbring et al. (1986) that the rarity (and now probable extinction) of reed-warblers on Aguijan may be the result of habitat destruction by feral goats. However, this has certainly not been the case on Alamagan where perhaps the densest population of reed-warblers still exists despite the fact that Alamagan is severely impacted by feral animals. The difference may be explained in the density of understory vegetation and amount of grassland, which, though not quantified, may be an order of magnitude greater on Alamagan.

It seems likely, given the known historic distribution of reed-warblers in the Marianas, that local extinctions are not uncommon. Nightingale

Reed-Warblers are known from only five of the southern ten islands (Fig. 1). Their distribution seems unrelated to local bird species diversity, habitat, or island area patterns. This patchy distribution is typical of the relictual pattern of a formerly widely distributed species and is typical of many bird species (including *Acrocephalus*) in both Micronesia and Polynesia (Pratt et al. 1987, Steadman 1989).

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CYPSELOIDES STORERI, A NEW SPECIES OF SWIFT FROM MEXICO

Adolfo G. Navarro S.,[1] A. Townsend Peterson,[2]
B. Patricia Escalante P.,[3] and Hesiquio Benítez D.[1]

Abstract.—A new species of swift (*Cypseloides storeri*) is described and given the English name White-fronted Swift. It apparently is most closely related to *C. cryptus* of Central America and northern South America. It is known from four specimens obtained in Michoacán and Guerrero in southwestern Mexico. *Received 6 June 1991, accepted 1 Sept. 1991.*

Resumen.—Se describe una especie nueva de vencejo (*Cypseloides storeri*), a la cual se le da el nombre común de Vencejo de Frente Blanca. Aparentemente, se encuentra muy cercanamente relacionado a *C. cryptus* de Centro y Sudamérica. Se conoce por cuatro especímenes recolectados en los estados de Michoacán y Guerrero en el suroeste de México.

Swifts are among the most poorly known families of birds. Several species new to science have been described relatively recently (e.g., Eisenmann and Lehmann 1962, Collins 1972), and many species are known from relatively few specimens. Here, we describe a new species of swift from the mountains of southwestern Mexico.

During the course of seven years of field work in the Sierra Madre del Sur of Guerrero by the Museo de Zoología (MZFC), one specimen of a medium-sized, dark swift was collected at Puerto del Gallo, a small ranch on the coastal slope of the Sierra de Atoyac of southern Guerrero. The bird was found clinging to a towel in camp late on a foggy night. Although it was initially identified as a Black Swift (*Cypseloides niger*), our examination of the specimen and comparisons with specimens of other swifts led us to conclude that the bird represents a new taxon. Study of other museum collections in Mexico revealed three additional specimens of the new form in the collection of the Escuela de Biología, Univ. Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán (UMSNH), all identified as Black Swifts by A. R. Phillips. Although species limits in the family as a whole, and especially in the genus *Cypseloides,* are notoriously difficult to define, our comparisons convince us that these four specimens are sufficiently distinct that they represent an undescribed species. We propose to call it:

[1] Museo de Zoología "Alfonso L. Herrera," Departamento de Biología, Facultad de Ciencias, Univ. Nacional Autónoma de México, Apartado Postal 70-399, México D.F. 04510 México.
[2] Museum of Natural Science, 119 Foster Hall, Louisiana State Univ., Baton Rouge, Louisiana 70803; (Present address: Div. of Birds, Field Museum of Natural History, Roosevelt Road at Lake Shore Dr., Chicago, Illinois 60605.)
[3] Dept. of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.

Cypseloides storeri, sp. nov.

WHITE-FRONTED SWIFT, VENCEJO DE CARA BLANCA

HOLOTYPE.—Museo de Zoología "Alfonso L. Herrera," Facultad de Ciencias, Univ. Nacional Autónoma de México (MZFC) 3535; male (left testis 3.1 × 1.5 mm) from Puerto del Gallo, Tlacotepec, Guerrero, Mexico, elevation 2500 m; collected by Julio Juárez on 2 September 1983, prepared by Adolfo G. Navarro S., field number AGNS 165.

DIAGNOSIS.—A medium-sized swift, sooty brown all over, with broad white frosting on the forehead, lores, and chin (Fig. 1). It is placed in *Cypseloides* and distinguished from swifts of other genera by the following criteria: from *Chaetura* by overall larger size, from *Streptoprocne* by smaller size and slender body form, and from *Aeronautes* and *Panyptila* by absence of large patches of white coloration on the body. It is distinguished from the Black Swift (*Cypseloides niger*) and the Sooty Swift (*C. "fumigatus"*) by the combination of relatively short wings (mean 136.6 mm ± 3.8 SE vs 151.5 ± 1.2 mm for *C. "fumigatus"* and 160.7 ± 1.5 mm for Mexican *C. niger*) and long tarsi (16.56 ± 0.91 mm vs 13.18 ± 0.21 mm for *C. fumigatus* and 12.67 ± 0.25 mm for Mexican *C. niger*), and from the Chestnut-collared Swift (*C. rutilus*) by absence of rusty brown coloration in the male and overall greater size (wing 136.6 ± 3.8 mm vs 124.2 ± 1.0 mm for *C. rutilus*). Although very similar in morphometric characters, it differs from *C. cryptus* most obviously in having a broad white frosting on the forehead, lores, and chin; in having whitish (as opposed to sooty) postorbital feathers; and in the gradually tapering (as opposed to more abrupt) shape of the face. *C. cryptus* has a restricted white chin patch, and occasionally white frosting on the lores, but never white on the center of the forehead. Sexual dichromatism appears negligible in the two male and one female specimens examined.

DISTRIBUTION.—Known from the mountains of southwestern Mexico, in the states of Michoacán (Tacámbaro) and Guerrero (Sierra de Atoyac), at elevations of 1500 and 2500 m, respectively.

DESCRIPTION OF HOLOTYPE.—General coloration is sepia (closest to color 119 of Smithe 1975), lighter on the underparts, and more blackish on the shoulders and the outer webs of the remiges and greater wing coverts. Feathers of forehead, lores, chin, and upper throat are tipped with white or whitish-buff with dark shaft-streaks, giving the appearance of a whitish face. The feathers immediately behind the eye are similarly frosted with white. The rostrum is tapered and somewhat elongated. The iris in life is dark brown, and the tarsi, toes, and bill are blackish sepia (in the preserved specimens).

MEASUREMENTS OF THE HOLOTYPE.—Bill length (anterior edge of nostril to tip) 4.8 mm, total exposed culmen 5.8 mm, wing chord 135 mm, tarsus 17.3 mm, tail 42.6 mm, and mass 39.5 g.

ETYMOLOGY.—We take pleasure in naming this species for Dr. Robert W. Storer in recognition of his many contributions to the knowledge of the birds of Guerrero and Michoacán.

SPECIMENS EXAMINED.—*Cypseloides storeri*: (MZFC holotype male) from type locality in Guerrero; Mexico: Michoacán, Salto de Santa Paula, 1–1.5 km NNE Tacámbaro (Univ. Michoacana San Nicolás de Hidalgo UMSNH 1 male, 1 female, 1 unsexed). The following specimens were compared with the holotype or all four specimens of *C. storeri*. *C. cherriei*: Venezuela: Aragua, Rancho Grande (American Museum of Natural History AMNH 1 female). *C. cryptus*: Belize: Manatee Lagoon (Univ. of Michigan Museum of Zoology UMMZ 2 males, 2 females); Nicaragua: Zelaya, El Recreo (University of California at Los Angeles Museum of Zoology UCLA 1 unsexed); Costa Rica: San Pedro (AMNH 1 female); Panama: Puerto Obaldía (Field Museum of Natural History FMNH 1 male); Pan-

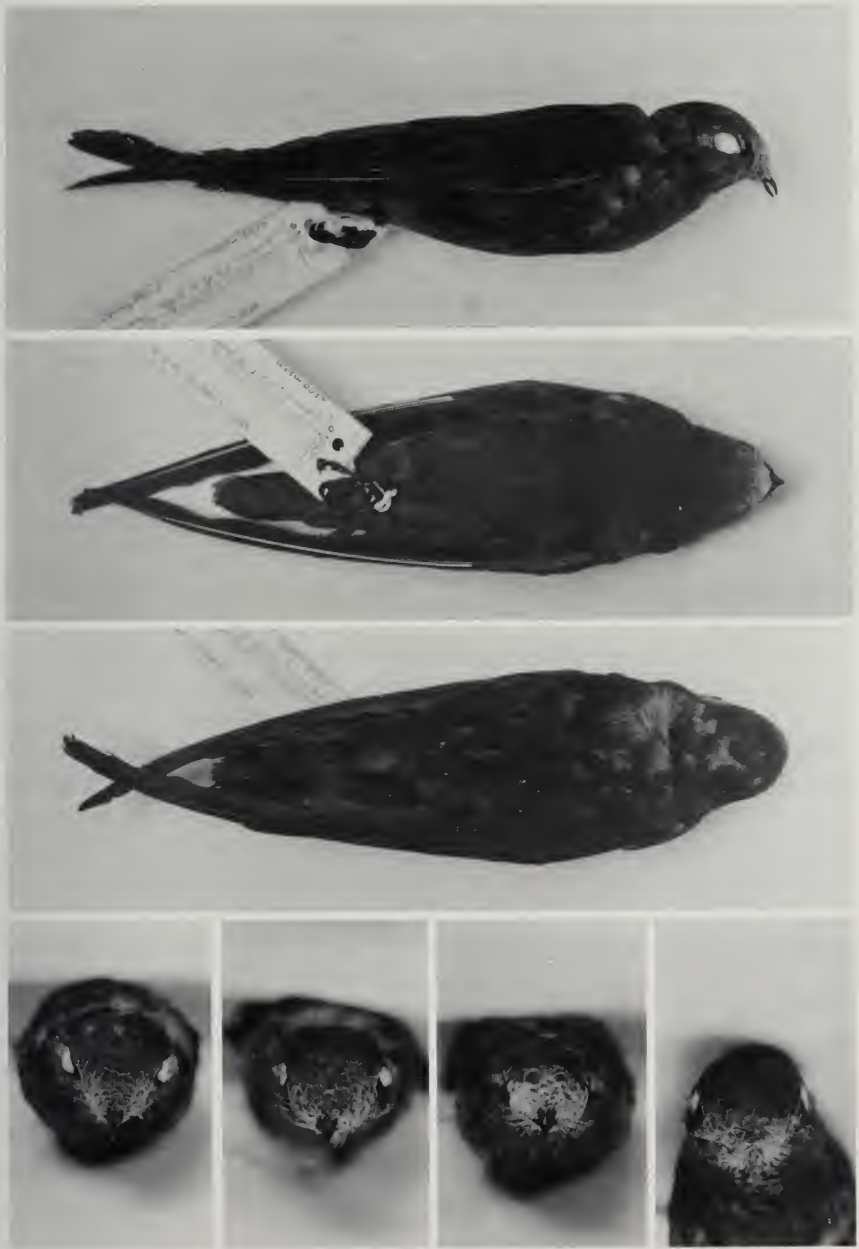

FIG. 1. Photographs of the holotype and three other specimens of *Cypseloides storeri*: holotype in side, ventral, and dorsal views (top-to-bottom), and head-on views of the holotype MZFC 3535, and UMSNH 1265, 1267, and 1266 (left-to-right).

ama: Hermosa Bay, Isla Coíba (Los Angeles County Museum of Natural History LACM 1 female); Peru: Puno, Abra de Maruncuca, 10 km SW San Juan del Oro (Louisiana State Univ. Museum of Natural Science LSUMZ 1 female). *C. senex*: Brasil: Pará, Serra do Cachimbo (LSUMZ 1 female). *C. major*: Argentina: Tucumán, Tapia (LSUMZ 1 male). *C. niger*: Mexico: Oaxaca, El Tule (Instituto de Biología, U.N.A.M. IBUNAM 1 male); Mexico: Oaxaca, Cerro San Felipe (AMNH 1 female); Mexico: Oaxaca, Colyotepec (IBUNAM 1 female); Mexico: Oaxaca, 4 mi E Matatlán (LSUMZ 1 male); Mexico: Morelos, Alpuyeca (AMNH 1 male); Mexico: Tlaxcala, 4 mi W Tlaxcala (Moore Laboratory of Zoology MLZ 1 male); Mexico? (IBUNAM 1 male); United States: Washington, Whitcom Co. (UCLA 1 female); Canada: British Columbia, Okanagan (UCLA 1 male); Cuba: Oriente, Tiguaba (UMMZ 1 male); Cuba: Guantanamo, San Carlos (UMMZ 1 male); Dominican Republic: Santo Domingo, La Vega (UMMZ 1 male). *C. rutilus*: Mexico: Oaxaca, Putla (IBUNAM 1 male); Mexico: Oaxaca, 1 mi E Putla (LSUMZ 2 males, 2 females); Mexico: Oaxaca, 1 mi SW Valle Nacional (LSUMZ 1 female); Mexico: Distrito Federal, Xochimilco (IBUNAM 1 male?); Mexico: Guerrero, Omiltemi (MZFC 1 female); Guatemala: Sierra de las Minas, 1 mi N Usumatlán (UMMZ 1 female); Guatemala: Tulumaje, Zecopa (LACM 1 female); Costa Rica: Hacienda El Pelón (UCLA 1 male, 1 female); Costa Rica: Irazú (FMNH 1 female); Peru: Puno, Sagrario (FMNH 2 females); Peru: Madre de Dios, Hacienda Amazonia (FMNH 3 females).

REMARKS

Within-population variation.—On inspection of the four specimens of *C. storeri,* we became concerned that variation in size might be too extensive for individuals of a single species. To test whether this seemingly elevated variation (Table 1) might indicate that the measurements were not drawn from populations of a single species, we compared it with levels of variation in a similar, closely related species. We used a series of 108 adult *C. rutilus* from Costa Rica (an area roughly equivalent to the known range of *C. storeri*) for which measurements of wing chord, tail, and tarsus were kindly provided by M. Marín (pers. comm.). (Restricting the data set to adults removes age-related variation from the *C. rutilus* but not from the *C. storeri* data, making the test conservative.) For each measurement, we bootstrapped estimates of the coefficient of variation (SD/mean) by selecting at random with replacement 1000 quartets of individuals from the *C. rutilus* data (selecting two males, one female, and one from both males and females, to replicate the sex ratio in the *C. storeri* sample), and calculating the coefficient of variation for each (Efron 1979). We then compared the coefficients of variation observed in *C. storeri* with the 95th percentile of the distribution of bootstrapped values for *C. rutilus.*

Coefficients of variation for *C. storeri* (N = 4) are 0.055, 0.061, and 0.028, for tarsus, tail, and wing chord, respectively. The bootstrapped distributions have their modes at 0.030, 0.038, and 0.024, and 95% limits (one-tailed test) at 0.076, 0.065, and 0.043. Hence, to the extent that variation in *C. rutilus* is representative of variation within other species of the genus, we have no grounds to reject the null hypothesis that four

TABLE 1

MEASUREMENTS (MM) OF THE FOUR SPECIMENS OF *CYPSELOIDES STORERI* AND OTHER *CYPSELOIDES* SWIFTS. SEXES ARE COMBINED IN THE CALCULATIONS OF MEANS. *C.* "*FUMIGATUS*" INCLUDES THE FORMS *MAJOR, ROTHSCHILDI,* AND *FUMIGATUS*

Taxon or specimen	N	Tarsus length	Tail length	Wing chord
Cypseloides storeri	4			
UMSNH 1265 (male)		15.25	47.0	140.0
UMSNH 1266 (unsexed)		16.65	48.5	139.5
UMSNH 1267 (female)		17.05	45.0	132.0
MZFC 3535 (male)		17.29	42.6	135.0
Mean ± SE		16.56 ± 0.91	45.8 ± 2.6	136.6 ± 3.8
C. cherriei	2	11.99 ± 0.58	43.4 ± 0.6	119.6 ± 1.6
C. senex	2	20.47 ± 0.05	46.0 ± 1.5	160.5 ± 2.5
C. cryptus	13	15.97 ± 0.31	46.9 ± 1.0	134.4 ± 1.3
C. niger USA	2	12.72	53.5 ± 1.5	160.0 ± 3.0
Mexico	7	12.67 ± 0.25	60.6 ± 2.4	160.7 ± 1.5
Costa Rica	3	11.83 ± 0.78	61.0 ± 2.5	151.0 ± 1.5
C. rutilus	18	11.96 ± 0.21	44.2 ± 0.7	124.2 ± 1.0
C. "*fumigatus*"	10	13.18 ± 0.21	51.5 ± 1.1	151.5 ± 1.2

measurements so different could be drawn from populations of a single species of *Cypseloides* swift.

Morphometric variation among species.—To understand morphometric variation in the *Cypseloides* swifts, we plotted measurements of tarsus, wing chord, and tail (Table 1; bill length not included because of low repeatability of measurements). The scatter of points (Fig. 2) reveals the distinctiveness of four groups of species in morphometric space: *C. niger* and *C.* "*fumigatus*" (including the forms *fumigatus, rothschildi,* and *major*) overlap somewhat, characterized by long wings and short tarsi; *C. senex* is distinctive in its overall large size; *C. rutilus* and *C. cherriei* group together because of their relatively small size in all characters; and finally *C. cryptus* and *C. storeri* are distinctive in their moderate size combined with relatively large tarsi. Further investigation omitting extreme taxa (e.g., *C. niger* and *C. senex*) and using principal components analysis failed to provide any additional resolution. Hence, on morphometric grounds, the closest relative of *C. storeri* appears to be *C. cryptus.*

Hybridization?—The species described here belongs to a most confusing genus. Because the characters of *C. storeri* are largely a mixture of characters of various swift species (e.g., white forehead as in some *C. niger,* size of *C. cryptus*), the possibility exists that these specimens actually represent hybrids between two other species, for instance, between *C.*

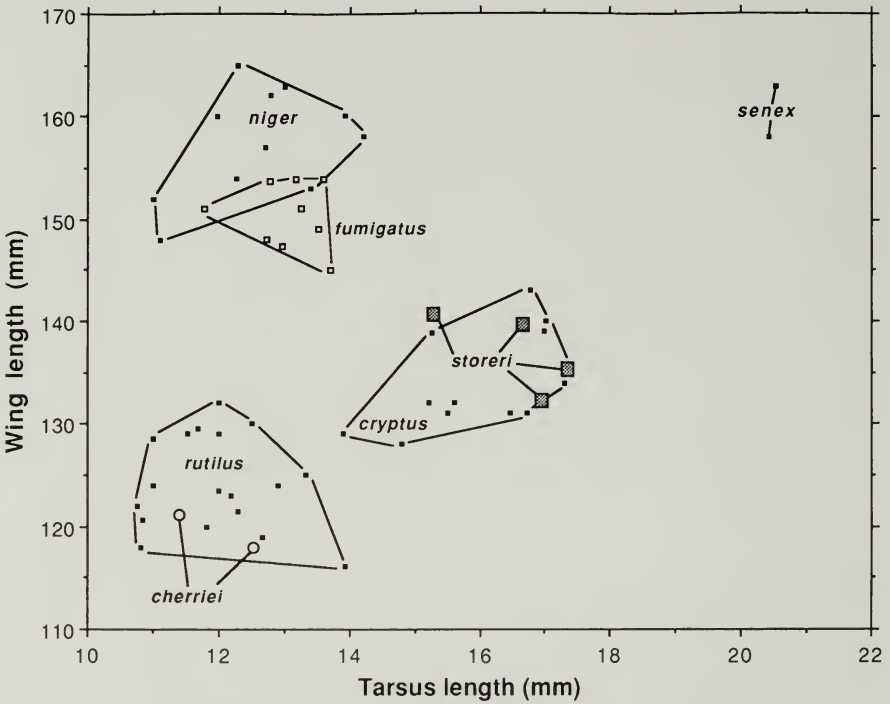

FIG. 2. Scatterplot of wing chord versus tarsus length for seven species of *Cypseloides* swifts. *C.* "*fumigatus*" includes the forms *major, rothschildi,* and *fumigatus.*

niger and *C. rutilus.* However, three points argue against this explanation. First, morphometric studies indicate *C. storeri* is in no way intermediate between any of the potential parental forms (Figs. 2 and 3). The measurements of *C. storeri* closely coincide with those of *C. cryptus,* and show no tendency towards any other of the species. Second, although *C. rutilus* occurs in the two localities from which *C. storeri* has been recorded, other potential parental forms are not known to breed there. *C. cryptus* is known from no closer than Belize and Honduras (the nearest breeding record is from Costa Rica; Marín and Stiles, in press); *C. niger* breeds along the western and southern mountains of Mexico, but the localities for *C. storeri* lie in an apparent distributional gap for the species (A.O.U. 1983). Finally, no example of hybridization between any species of swifts is known (C. T. Collins, pers. comm.). Hence, neither the opportunity (i.e., sympatry of parental forms), nor evidence (e.g., morphological intermediacy) for a hybrid origin exists in the present case, and we consider a hybrid origin to be unlikely.

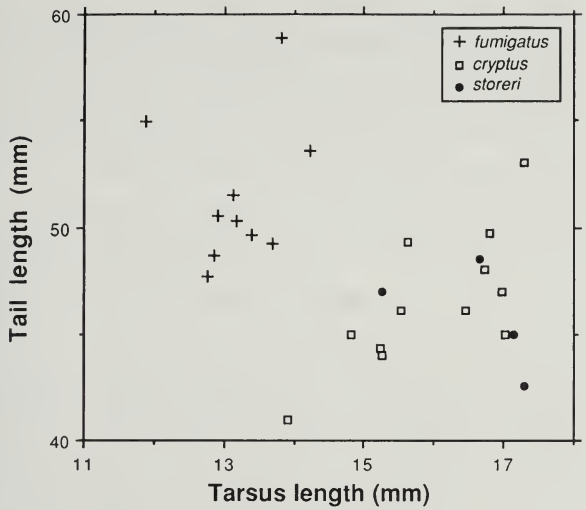

FIG. 3. Scatterplot of tail length versus tarsus length for the complex of species including *Cypseloides "fumigatus," C. cryptus,* and *C. storeri.*

Taxonomic status.—Species limits in swifts have presented a number of challenges to ornithologists: characters are often subtle differences in shape or coloration; specimens are scarce, making analysis of variation due to sex, age, and geography difficult; and little is known about swift biology in general. The form described herein is closely similar to the mid-sized swifts *C. cryptus* of Central America and northern South America and *C. "fumigatus"* (itself a taxonomic mess) of southern South America. Although the specific distinctiveness of *C. cryptus* from *C. fumigatus* has been questioned (Marín and Stiles, in press), they are distinct in morphometric space (Fig. 3). The four specimens of what we describe as *C. storeri* represent a population of swifts most similar to *C. cryptus.* The two forms are disjunct by about 1500 km. They differ markedly in the amount of white on the face: *C. cryptus* usually shows a small white patch on the chin, and some individuals show white on the lores; all four specimens of *C. storeri* have extensive white on the chin, lores, and forehead. (The difference in facial shape mentioned above is consistent in the three specimens of *C. storeri* for which the cranium is intact in the skin, but the reliability of this character will have to be checked when skeletal series are available.) We recognize that under some taxonomic viewpoints, the new form described here might better be considered a subspecies or a member of a superspecies complex. However, in view of the large range disjunction and the non-overlapping character distribution, considering that the current tendency of the ornithological community is to split

differentiated allopatric populations (J. V. Remsen, pers. comm.), and because genetic studies increasingly support the distinctiveness of such disjunct populations (e.g., in the Scrub Jay [*Aphelocoma coerulescens*], Peterson 1990; Common Bush-Tanager [*Chlorospingus ophthalmicus*] and Chestnut-capped Brush-Finch [*Atlapetes brunneinucha*], Peterson et al., in press), we argue that *C. storeri* merits specific rank.

Ecological information.—The two localities from which *C. storeri* is known suggest that the species occurs in mountainous areas with high waterfalls and deep canyons. The Guerrero specimen probably was attracted to lights in camp, so nothing is known about the location of the breeding site; still, the locality is in montane cloud forest with deep canyons, rushing streams, and waterfalls. The Michoacán specimens were taken from an ecotone between pine-oak forest and dry, tropical deciduous forest in an area with many high waterfalls. Information on the ecological relationships of *C. storeri* with other swift species is scant; however, in both localities, White-naped Swift (*Streptoprocne semicollaris*), Chestnut-collared Swift, Vaux's Swift (*Chaetura vauxi*), White-throated Swift (*Aeronautes saxatalis*), and Great Swallow-tailed Swift (*Panyptila sanctihieronymi*) have been sighted.

No *storeri*-like swifts have been seen by us in many months of additional field work in the Sierra de Atoyac and other parts of central and southern Guerrero. However, during two days of field work in October 1990 at several high waterfalls near Tacámbaro, Michoacán, we sighted four individual swifts that appeared to be *C. storeri*. At about 18:00 h (nightfall), after large flocks of White-naped Swifts and a few Chestnut-collared Swifts had entered the canyon for the night, four swifts intermediate in size between the latter two species entered the canyon flying low along the treetops. Although the sighting was brief, and the swifts could not be located later at the waterfall roost site itself, we believe that these individuals belong to the new species.

Biogeography.—The presence of this new taxon in the mountains of western Mexico supports the idea that these mountain systems are important as centers of endemism (Escalante et al., in press). Other species endemic to the mountains of western Mexico include Pileated Flycatcher (*Xenotriccus mexicanus*), Eared Poorwill (*Nyctiphrynus mcleodii*), Guerrero Hummingbird (*Eupherusa poliocerca*), Flammulated Flycatcher (*Deltarhynchus flammulatus*), White-throated Jay (*Cyanolyca mirabilis*), and Black-throated Magpie-Jay (*Calocitta colliei*) (A.O.U. 1983). Moreover, as with the White-fronted Swift and the White-chinned Swift, many western Mexican forms are disjunct outliers with close relatives in Central America or northern South America, such as Mexican Woodnymph

(*Thalurania ridgwayi*) and Crowned Woodnymph (*T. colombica*) (Escalante and Peterson, in press), Short-crested Coquette (*Lophornis brachylopha*) and Rufous-crested Coquette (*L. delattrei*) (Banks 1990), White-throated Jay and Silvery-throated Jay (*C. argentigula*), Red-breasted Chat (*Granatellus venustus*) and Rose-breasted Chat (*G. pelzelni*), and northern and southern populations of Rosy Thrush-Tanager (*Rhodinocichla rosea*) and Military Macaw (*Ara militaris*). This repeated distributional and phylogenetic pattern suggests a previous biogeographic relationship between western Mexico and Central America.

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BREEDING BEHAVIOR OF THE GREEN-RUMPED PARROTLET

JAMES R. WALTMAN[1] AND STEVEN R. BEISSINGER[1,2]

ABSTRACT.—We studied the breeding behavior of Green-rumped Parrotlets (*Forpus passerinus*) using nest boxes in the llanos of Venezuela. Aggressive and courtship displays, and nest prospecting behavior are described. Females occupied nest boxes for about 80% of daylight hours from shortly before egg laying through hatching (30–40 days), and did all incubating and brooding. Males spent nearly 80% of the time away from the nest, presumably foraging for their mates and chicks. Clutch sizes of females were correlated positively with the rate at which they were fed by males during egg laying. Clutches hatched asynchronously, and nestling growth and development was slow. Females stopped brooding when oldest chicks were one to two weeks of age to join their mates in feeding young, though the youngest chicks were at most a few days old. Food delivery rates by parents to young were related positively to brood size after all eggs had hatched. Most pairs (91%) remained mated throughout the breeding season. Mate replacement between years was more common (≥31%). More than half of the females that nested in the first part of the breeding season attempted second nests. Intervals between nesting attempts ($\bar{x}$ = 22 days) were correlated positively with the number of young fledging from first nests. Over three-quarters of the pairs that remained together and renested used the same nest box, even though intruders constantly attempted to obtain nest sites. Results are discussed in relation to the division of parental care and the high degree of pair cohesion exhibited by parrots. *Received 9 April 1991, accepted 1 Oct. 1991.*

Little is known about the breeding biology of the Green-rumped Parrotlet (*Forpus passerinus*), one of seven species in the Neotropical genus *Forpus*. Green-rumped Parrotlets inhabit lowland wet and dry forests, savannah, and farmlands (Friedman and Smith 1950, Forshaw 1989). During the rainy season, nests are made in unlined natural tree cavities in holes excavated in arboreal termitaria (Belcher and Smooker 1936, Friedman and Smith 1950, Forshaw 1989), and in cavities in wooden fence posts (Beissinger and Bucher 1991). One unusual nest was in a hole at the base of a palm frond (Belcher and Smooker 1936) and another was in the cross-arm of a clothesline support (Friedman and Smith 1955). Clutches of captive pairs usually range between four and six eggs, but up to 10 eggs have been recorded (Wildeboer 1926, Enehjelm 1951, Noble 1984). During the dry season, breeding appears to cease and flocks of more than 100 birds can be seen (Morton 1979).

This paper presents new information on the breeding biology and food

[1] School of Forestry and Environmental Studies, Yale Univ., 205 Prospect Street, New Haven, Connecticut 06511. (Present address JRW: National Audubon Society, 666 Pennsylvania Avenue, S.E., Suite 200, Washington, D.C. 20003.)
[2] Dept. of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008.

habits of the Green-rumped Parrotlet in the llanos of Venezuela. We also present some information on the bird's behavior in the dry season.

STUDY AREA AND METHODS

We studied Green-rumped Parrotlets on the cattle ranch Hato Masaguaral, 45 km south of Calabozo, in Guarico, Venezuela (8°34'N, 67°35'W). The study area is mostly flat natural savanna, or llanos, with scattered clumps of mature trees. Vast areas flood seasonally in the wet season (June–November) and dry out in the dry season (December–May) (Troth 1979, Beissinger et al. 1988). We conducted field work from June to December, 1988, and during the last two weeks of March, 1989. Additional sightings of banded birds were made from June to December, 1989 as part of other studies (Beissinger and Stoleson, in press). Rainfall measured 139 cm during the study in 1988 and there was no rain during the fieldwork in March, 1989.

Forty nest boxes, made from polyvinyl-chloride plastic, were attached to fence posts frequently used by nesting Green-rumped Parrotlets (Beissinger and Bucher 1991). The boxes were opened and observations were begun on 21 June, 1988. At that time no active nests were found but about 15 to 20 pairs were prospecting for nest sites in fence posts. Adult birds were caught in 12-m mist nets near active nests along fencelines, and uniquely banded with plastic color and aluminum bands.

Nest boxes were checked every one to two days for activity and contents. Eggs were uniquely marked with indelible ink, weighed to the nearest 0.1 g with a 10-g Pesola scale, and measured for length and width to the nearest 0.01 mm with dial calipers. Egg volume was calculated from Hoyt's (1979) equation: volume = (0.51) × (egg length) × (egg width)^2. Hatchlings were weighed to the nearest 0.1 g with a 10-g Pesola scale and marked on their toe nails with a unique color of fingernail polish. Nestlings were reweiged to the nearest 0.1 and 0.5 g with 10-g and 30-g Pesola scales every two–five days until fledging. We banded nestlings near day 20 with a unique combination of colored plastic and aluminum bands. Nestlings were considered to have fledged if they survived in the nest until at least 25 days of age.

We observed nests from 30 to 50 m with a 15–40× telescope and 10× binoculars for two to four hour periods throughout the nesting cycle between 07:00 and 13:00 h. Sex of parents was differentiated by plumage dichromatism (Forshaw 1989). The locations of parents were noted as "inside the nest cavity," "in the nest area" (within a ten-m radius of the nest), or "outside the nest area." The presence of conspecifics and other birds in the nest area was recorded. Courtship, parental and nest defense behaviors were recorded for each parent. Twenty-five active nests were observed at least once and sixteen nests were observed at least four times, generally at 7 to 10 day intervals. We made a total of 99 nest watches totaling 295 h.

During our watches, *F. passerinus* often disappeared from view, either outside the nest area or inside the nest cavity, and it was difficult to be sure if birds fed their mates or young when feedings were not in view. However, males often had seeds on their bills after emerging from the cavity or after returning to the nest area with their mates. Therefore, we assumed that males fed egg-laying, incubating, and brooding females whenever the male returned after at least 10 minutes away from the nest area and then disappeared with the female either into the cavity or away from the nest. Females were assumed to have foraged for themselves if they were seen foraging or disappeared from the nest area for more than ten minutes. When nests contained young, parents often had seeds on their bills and frequently shook their heads in a pre-regurgitation motion before entering the box. Occasionally, nestling begging calls could be heard from inside the boxes. Thus, we assumed that nestlings

were fed whenever a parent returned from a trip away from the area of at least 10 min duration, and then entered the nest or passed food to a mate which subsequently entered the nest. Visits by each parent to nests with young were scored as separate feeding bouts.

Observations of diet, vocalization, flocking, and roosting behavior were made ad libitum during nest observations, nest checks, mist netting, and periodic walks through the study area.

Clutch sizes were categorized as small (5–6 eggs), medium (7–8 eggs), and large (9–10 eggs). Likewise, brood sizes were defined as small (1–5 young), medium (6–7 young), and large (8–10 young). The nesting cycle was divided into six periods: courtship, egg laying, incubation, hatching, nestling, and fledging.

Data were analyzed using SYSTAT (Wilkinson 1990). Means are reported with standard deviations. Percentages were arcsin-transformed to normalize the distribution. When data were normally distributed and variances were equal, analyses of variance (ANOVA), and *t*-tests were used to compare behaviors of parents among different periods and among different-sized clutches and broods. The Spearman rank correlation was used with non-parametric data. Logistic curves and growth parameters were fit to weights from chicks of known age with empty or nearly empty crops using the SAS NLIN procedure (SAS 1988).

RESULTS

Nest prospecting.—Individual pairs prospected at up to six nest sites before deciding on a cavity. Pairs flew to potential nest sites together up to 10 times per hour. Upon arriving at a potential nest site, prospecting pairs were usually very vocal, emitting a loud "rapid chatter" of indistinct notes, similar to the twittering of Budgerigars (*Melopsittacus undulatus*) (Forshaw 1989).

While prospecting at nest sites, pairs were often accompanied by and fought with additional pairs and unmated males. Birds gave a threat display by spreading wings, expanding plumage, and crouching with bills opened and tails fanned. Birds lunged at one another, usually with bills opened wide and feet clutching at a perch and occasionally grasped one another with bills or feet. A penetrating "tsup-tsup" call, described by Snyder (1966), often accompanied these encounters. *F. passerinus* occasionally behaved aggressively towards other species at nest sites, particularly Saffron Finches (*Sicalis flaveola*). Saffron Finches, Straight-billed Woodcreepers (*Xiphorhychus picus*), Spot-breasted Woodpeckers (*Chrysoptilus punctigula*) and Dusky-capped Flycatchers (*Myiarchus tuberculifer*) all nested in fence posts. *S. flaveola* and *M. tuberculifer* occasionally nested in the *Forpus* nest boxes.

Courtship behavior.—Several ritualized head, tail, and wing movements were initiated by both sexes throughout the nesting cycle, but occurred most frequently during the courtship period. These courtship displays, described below, often preceded or followed the entrance of one or both members of a pair into the cavity. In the early stages of prospecting, it was usual for birds to enter cavities singly while their mates waited outside.

During "head bowing" displays, the body was bent forward and the head was rocked up and down, usually but not always into or towards an opening of a potential nest cavity. The tail was sometimes tipped into the air as the head was directed downward. Bouts of head bowing typically lasted from a few seconds to 1.5 min ($\bar{x}$ = 23.8 ± 13.3 sec, range = 5–100 sec, N = 62). Birds bowed alone or facing their mate, alternating downstrokes between pair members.

"Tail fanning" usually accompanied head bowing. Tail feathers were spread in a fan-like manner for up to 30 sec, or were alternately fanned and relaxed for only a second or two at a time. Tail fanning bouts averaged 18.2 ± 11.2 sec (range = 2–100 sec, N = 48).

"Wing flashing" was performed almost exclusively by males in the presence of females or other males, usually, but not always, at a potential nest site or before copulation. Three types of wing flashing were discernible: quick flicks, full spread and shake, and slow lifts. During "quick flicks," described by Arman and Arman (1980) and Snyder et al. (1987), the wings were quickly spread and refolded, revealing a flash of blue underwing color for less than a second. Bouts of "quick flicks" ranged from 1 to 129 sec ($\bar{x}$ = 18.1 ± 32.1 sec, N = 56). Females occasionally performed "quick flicks" when fighting with conspecifics at a nest site, even though females lack the contrasting blue underwing of males. "Full spread and shake" was observed on only six occasions, always performed by males before a group of one or more females and one or more other males. Wings were fully extended to the sides and then rapidly moved forward and back, no more than a few centimeters, for 6 to 250 sec ($\bar{x}$ = 120.8 ± 115.4 sec, N = 6). This action produced a blur of brilliant blue from the underwing.

"Slow lifts" were also performed by solitary males perched in trees often within 20 m of an active nest. The folded wings were slowly lifted a few centimeters and rotated outward slightly, revealing the blue underwing. Wings were extended in this manner for only 2 or 3 sec at a time. "Slow lift" bouts ranged from 1 to 58 sec ($\bar{x}$ = 21 ± 21.3 sec, N = 8). "Slow lifts" were usually accompanied by a shrill "chee . . . chee . . . chee," consisting of three to seven notes (Friedman and Smith 1950). Males called in this way to females in a nest cavity. We believe that females may recognize their mates' calls because females usually climbed to the cavity opening when their own mates called but not when other males called.

Two types of bill contact were observed within pairs. Pairs often engaged in "nipping bouts" at a potential nest site, especially during agonistic encounters. Pairs typically lunged at one another's bills, legs, and feet, poking and nipping at the flesh in a manner suggesting heightened allo-

preening. Nipping bouts lasted between 4 and 24 sec ($\bar{x}$ = 10.7 ± 5.5 sec, N = 38). Pair members often "allopreened" their mates in the head and neck regions. Allopreening bouts often were mutual preening bouts and ranged from 4 to 309 sec ($\bar{x}$ = 45.4 ± 53.2 sec, N = 102).

"Courtship feeding" was observed on fence lines within 5 m of the nest cavity and in vegetation within 40 m of nests. Females begged to initiate courtship feeding by crouching forward, fully opening their bills, and rocking their heads up and down rhythmically. Feeding bouts lasted between 6 and 88 sec ($\bar{x}$ = 26.5 ± 19.9 sec, N = 33) and were occasionally punctuated with a high pitched scream emitted by the female. Prior to feeding females, males began regurgitation by rotating their heads in an elliptical manner from side to side. Food was delivered with bills clasped at right angles. Afterwards, regurgitated seeds were frequently observed on the male's bill.

F. passerinus fed mostly on forbs and grasses, especially *Croton hirtus, Hyptis suaveolens, Wissadula* sp., *Cyperus* spp., *Scoparia dulcis,* and *Melochia parviflora. C. hirtus* occurred most often in the crops of nestlings. Parrotlets also occasionally fed on seeds from the fruits of trees, such as *Anona* sp. and guava (*Psidium guava*). Most birds foraged in small flocks of 3–20 individuals, but in the dry season, *F. passerinus* foraged in flocks of over 100 individuals.

Sometimes pair members locked their bills together as if courtship feeding but without the preceding male regurgitation or female begging motions characteristic of feeding bouts. These "bill clasping" episodes were witnessed only during the courtship and egg-laying periods and lasted between 28 and 168 sec ($\bar{x}$ = 53.6 ± 55.5 sec, N = 9). It was difficult to determine whether food passage occurred at these times or whether "bill clasping" was another courtship behavior. Bouts of "bill clasping" were distinct from normal courtship feeding bouts, which were usually composed of a series of short bill grasps separated by regurgitation and begging.

Copulation occurred in trees within 40 m of the nest and rarely on fence lines. Begging and courtship feeding often preceded copulation. Males typically "quick flicked" or "full spread" their wings while walking towards the female, and often engaged in "nipping bouts" before mounting. Copulation behavior was typical for New World parrots (Smith 1975, Skeate 1984, Snyder et al. 1987), except that the male often grasped the female's primaries while mounting rather than placing one foot passively on her back. Copulations lasted between 63 and 205 sec ($\bar{x}$ = 91.9 ± 34.3 sec, N = 17), and occurred from seven days before egg laying began until six days after egg laying had ceased. After copulation, a pair often engaged in allopreening before returning to the nest cavity.

Nest site attachment and occupancy.—Ownership of a nest site was

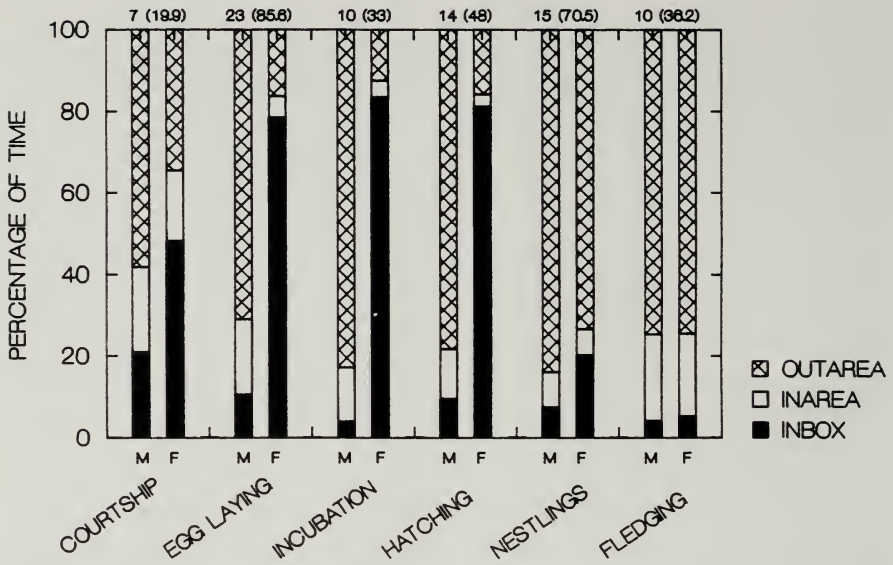

FIG. 1. Percentage of daylight hours that male (M) and female (F) *Forpus passerinus* parents spent in three locations during the six periods of the nesting cycle. Dark bars represent time spent in nest cavities, open bars represent time spent in the nest area and crosshatched bars represent time spent out of the nest area. Number of observation periods (total h of observation) are depicted by numbers above the bars.

established when both members of a pair entered the cavity together and remained inside for minutes at a time. Time budgets of males and females became quite different as egg laying approached and remained different well into the nestling period. Males spent progressively more time away from their nests while females spent most of their time in the nest until all of their eggs hatched (Fig. 1). A three-way ANOVA (Table 1) showed that the percentage of time that parents spent in, near, and away from the nest (location) differed significantly. Location interacted with sex and nesting period, indicating that the sexes differed in their locations during some periods of the nesting cycle but not during others (Table 1, Fig. 1).

A few days before egg laying, females began spending about 75% of the time in the cavity (Fig. 1) and roosted alone there at night. Males made solitary flights away from the cavity at this time, presumably to forage, and continued roosting in large trees near nesting areas in groups of 7 to 43 (N = 8 roosts). The number of individuals at roosts during the nesting season was small compared to dry season roosts, attended by up to 159 individuals of both sexes ($\bar{x}$ = 64 ± 61 individuals, N = 4 roosts).

Egg laying and incubation.—In 1988, egg laying began on 12 July, three

TABLE 1

ANOVA OF THE ARCSIN-TRANSFORMED PERCENTAGE OF TIME THAT MALE AND FEMALE *FORPUS PASSERINUS* PARENTS SPENT IN THREE LOCATIONS DURING THE SIX DIFFERENT PERIODS IN THE NESTING CYCLE (FIG. 1)

Effect	df	*F*	*P*
Sex of parent	1	0.3	0.60
Location[a]	2	266.5	0.01
Period[a]	5	0.3	0.92
Sex·location	2	231.5	0.01
Sex·period	5	0.2	0.98
Period·location	10	32.4	0.01
Sex·period·location	10	26.0	0.01
Error[b]	408		

[a] See methods section for definition of periods of the nesting cycle and location.
[b] See Figure 1 for sample sizes.

weeks after pairs were first seen entering nest cavities. The last clutch was initiated on 10 November (Fig. 2), although two pairs were prospecting for nest sites on 6 December, the last day of the study. Sixty-three nesting attempts were observed: 58 in nest boxes and five in fence posts.

Eggs were white and spherical to elliptical in shape, with one end slightly more pointed than the other. Egg lengths averaged 18.0 ± 0.8 mm (range = 16.1–20.7 mm, N = 280), egg widths averaged 15.1 ± 0.5 mm (range = 13.4–16.1 mm, N = 280), and egg volumes averaged 2084 ± 184.1 mm^3 (range = 1479–2621 mm^3, N = 280). Egg masses, taken up to two days after laying, averaged 2.2 ± 0.3 g (range = 1.6–2.8 g, N = 42).

Clutches averaged seven eggs and were laid over a seven to 16 day period (Beissinger and Waltman 1991). Eggs were usually laid on successive days or every other day, but occasionally at intervals up to five days. Females initiated incubation with their first egg (Beissinger and Waltman 1991) and during the egg-laying period spent over three-fourths of the day inside the cavity ($\bar{x}$ = 79 ± 21%, range = 4–100%, N = 85.6 h at 23 nests, Fig. 1).

Males visited females up to three times an hour to feed, preen, and copulate with them. Pairs continued courtship behaviors during these visits. On average, males fed females 0.97 ± 0.44 times per hour (N = 85.6 h at 23 nests) during the egg-laying period (Fig. 3). The rate at which males fed females during this period (Fig. 4) was positively correlated with the eventual clutch size of their mates (Spearman $r = 0.5$, $P < 0.05$, N = 21 nests).

Incubation was performed exclusively by females. Females spent 84 ±

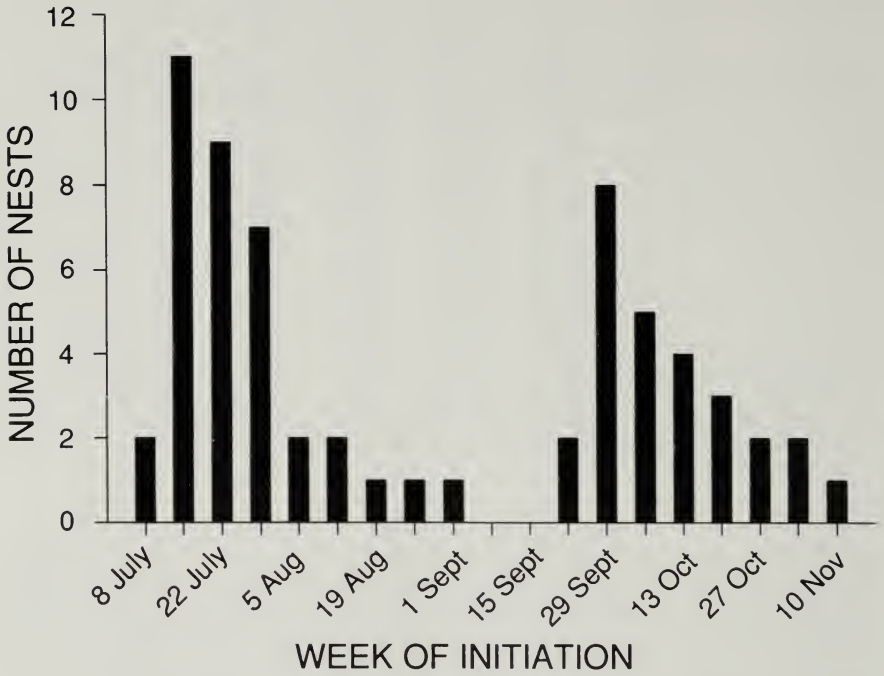

FIG. 2. The number of *Forpus passerinus* nests initiated during each week of the study. Nests were initiated when the first egg was laid.

15% of the daytime in nests during this period (range = 60–100%, N = 33 h at 10 nests, Fig. 1) and developed large brood patches. Males were seen at nests less frequently than in the preceding periods (Fig. 1) and fed their females slightly less often ($t = 1.5$, $P = 0.15$) during incubation ($\bar{x} = 0.74 \pm 0.36$ feeds per hour, N = 33 h at 10 nests, Fig. 3) than during egg laying. The rate of food deliveries by males to their mates did not correlate with clutch size during the incubation period (Spearman $r = 0.20$, $P > 0.5$, N = 10 nests).

Parental care.—Eggs hatched asynchronously 18 to 22 days after laying (Beissinger and Waltman 1991). Two to fourteen days passed between the hatching of first and last nestlings and an average of 5.7 chicks hatched per brood (Beissinger and Waltman 1991). Egg shells were not removed from nests after hatching and were often found buried under nest material.

Parental feeding rates differed significantly between the sexes, by nesting periods, and for brood sizes (Table 2, Fig. 3). Males apparently did all or most of the foraging for the nestlings in the hatching period, and passed food either directly to their young or to their mates. Males made almost

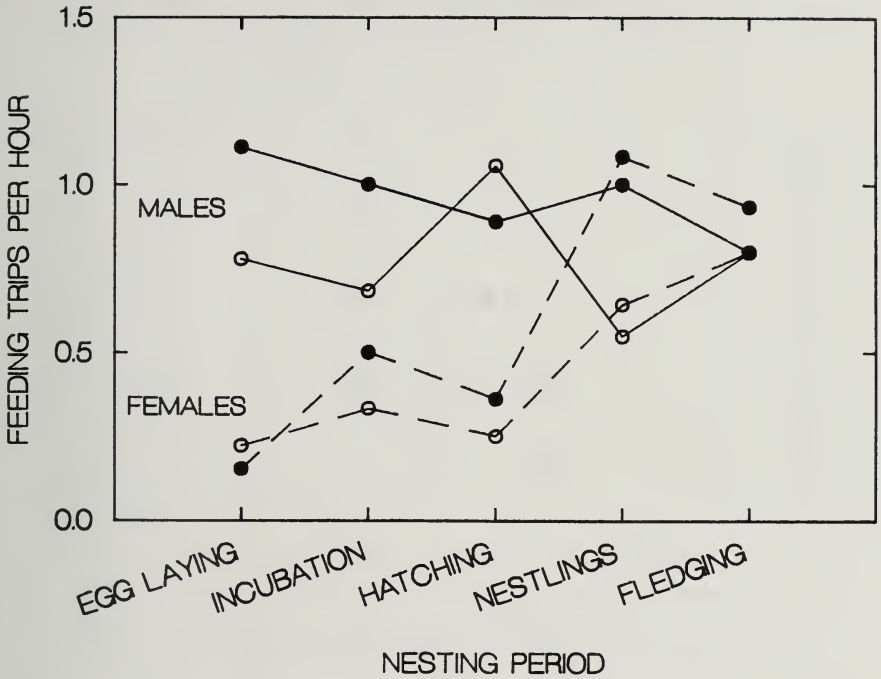

FIG. 3. Feeding rate by *Forpus passerinus* males (solid lines) and females (broken lines) at nests containing medium (solid circles) and small (open circles) broods during five periods of the nesting cycle.

one feeding trip to the nest each hour during this period ($\bar{x} = 0.93 \pm 0.23$ feedings/h, N = 48 h at 14 nests) (Fig. 3). Females fed nestlings infrequently during the hatching period ($\bar{x} = 0.28 \pm 0.22$ feedings/h, N = 48 h at 14 nests) (Fig. 3). Females brooded nestlings most of the day ($\bar{x} = 81.2 \pm 10.4\%$, N = 48 h at 14 nests) until the oldest chick was between one and two weeks old (Figs. 1 and 5). Females continued roosting in nests overnight until the youngest chick was in its second week.

After brooding was completed, males and females nearly always visited nests together. Both sexes spent a majority of time away from the nest area (Fig. 1). On average, males and females fed their young just less than once an hour during the nestling period (males: $\bar{x} = 0.76 \pm 0.27$ feedings/h; females: $\bar{x} = 0.86 \pm 0.31$ feedings/h, N = 70.5 h at 15 nests) (Fig. 3). The number of feeding visits per hour at 15 nests by males (Spearman $r = 0.75$, $P < 0.01$), females ($r = 0.69$, $P < 0.01$), and pairs (male + female rate; $r = 0.77$, $P < 0.01$) were positively correlated with brood size during the nestling period. During the fledging period, parents continued to show

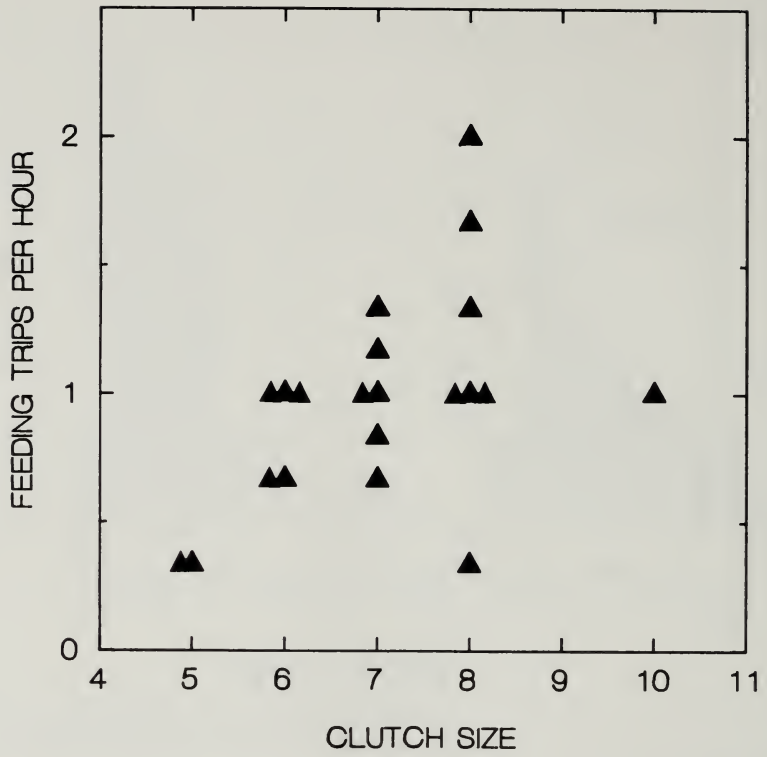

FIG. 4. Food delivery rates by *Forpus passerinus* males to females during the egg-laying period as a function of ultimate clutch size.

TABLE 2

ANOVA OF PRESUMED FEEDING RATE AT NESTS BY MALE AND FEMALE *FORPUS PASSERINUS* PARENTS HATCHING SMALL AND MEDIUM-SIZED BROODS

Effect	df	*F*	*P*
Brood size[a]	1	9.4	0.01
Sex of parent	1	29.3	0.01
Period[a]	4	3.6	0.02
Size·sex	1	0.1	0.72
Size·period	4	2.0	0.11
Sex·period	4	10.3	0.01
Size·sex·period	4	1.5	0.21
Error	98		

[a] See methods section for definition of brood sizes and periods of the nesting cycle.

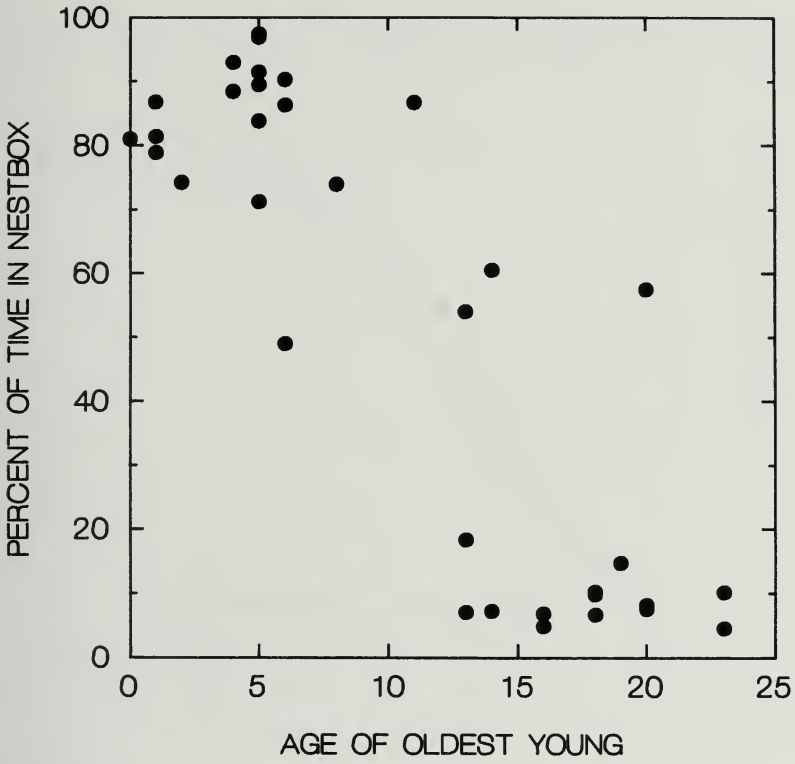

FIG. 5. Percentage of daylight hours that *Forpus passerinus* females spent in the nest cavity in relation to age of the oldest nestling.

the same pattern of nest visitation and feeding (Figs. 1 and 3). Adults may also have been feeding fledged young away from the nest at this time.

Nestling growth and development.—At hatching, nestlings weighed between 0.8 and 2.8 g ($\bar{x}$ = 1.8 ± 0.3 g, N = 170). Chicks were born with eyelids fused and only a small amount of yellow or white down. Eyes did not begin to open until six to eight days after hatching, and were not fully opened until day 8–10. Primary feather shafts began to emerge on day 8–10 and feathers began erupting on day 15–20. Green feather coloration was visible, and blue color was seen in male nestlings on or about day 16–23. After about 25 days, plumage of nestlings was nearly indistinguishable from that of adults.

Nestling growth was quite slow (Fig. 6) and resembled the logistic curve reported for other parrots (Bucher 1983, Navarro and Bucher 1990). The average daily growth increment (K) for all chicks was 0.233 ± 0.005 g,

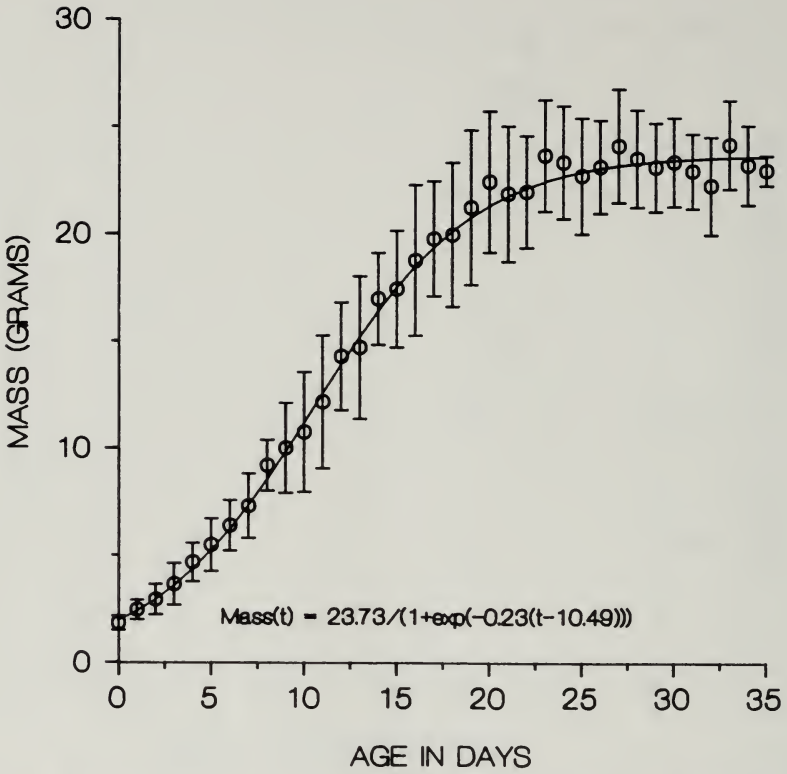

FIG. 6. Mean and standard deviation of mass for *Forpus passerinus* nestlings with empty or nearly empty crops. Sample sizes (totalling 1128 masses) vary from 2 to 165 and averaged 41 ± 28. The logistic curve was plotted using the parameters given in the equation on the figure.

the inflection point (I) was reached at age 10.48 ± 0.12 days, and the asymptotic mass (A) averaged 23.7 ± 0.2 g based on 1128 masses. Growth parameters did not differ between males (K = 0.236 ± 0.008 g, I = 10.16 ± 0.16 days, A = 23.7 ± 0.2 g, N = 480) and females (K = 0.235 ± 0.007 g, I = 10.17 ± 0.15 days, A = 23.9 ± 0.2 g, N = 466).

Nestlings remained in the bottom of the cavity until their third week, when they began to climb to the nest opening to receive food. Often, some nestlings would beg at the cavity opening while others remained inside. Parents often fed the young at the cavity entrance but would also enter the cavity to feed nestlings inside.

Fledging occurred 28 to 35 days after hatching, and the interval between the fledging of first and last chicks averaged 9.1 days (Beissinger and Waltman 1991). Three times we observed first flights of fledglings. In

each case, the parents urged the young out of the nest by flying from the nest opening back and forth to a perch a short distance away. Fledglings flew about 10–30 m to perch in a tree, accompanied in each case by the parents.

We occasionally witnessed parents feeding fledged young. Fledglings rarely followed their parents back to the nest. We observed only one female feed a fledgling while nestlings remained in her nest. This fledgling was 32 days old and had fledged two days earlier. On three occasions we observed parents being pursued by their entire post-fledged brood away from the nesting area. In each case, the parents fed at least one of the young. The young were 37 to 56 days old and had fledged seven to 22 days earlier. More often, fledglings were resighted in small flocks foraging with five to 20 other birds, including other yearlings. They also appeared occasionally at other nests and begged to the parents there.

Nestling mortality.—Of the 63 nesting attempts that we observed in this study, 23 failed before at least one young fledged. Probable causes of these failures include: predation (five nests), abandonment due to harassment from a neighboring pair (three nests), abandonment caused by human interference (three nests), flooding of the nest structure (two nests), and death or disappearance of one parent (two nests). Eight nests were abandoned for unknown reasons. Snakes, lizards, and rodents were common in the study area and could have accounted for nest predation. We also found a small marsupial (*Marmosa robinsoni*) in nest boxes on three occasions.

Causes of mortality of nestlings at successful nests were difficult to determine. Starvation may have killed all last and penultimately hatched nestlings, which were found dead in nests with empty crops. In contrast, only 60% of the earlier hatched nestlings died with empty crops (Beissinger and Waltman 1991). Three chicks were found dead in a nest with very full crops and wet plumage. Because these nestlings were between 17 and 25 days old, it is possible that they had put their heads out of the nest opening to beg for food, were rained on, and died of hypothermia. Three nestlings were found dead with punctures on the head, neck and back, and with broken, twisted wings. Similar wounds have been observed when invading pairs commit infanticide (S. H. Stoleson, pers. comm.). On average, 4.7 nestlings fledged from successful nests (Beissinger and Waltman 1991).

Renesting.—Nest initiations occurred in two waves during the 1988 breeding season (Fig. 2). The initial period lasted from 12 July through 2 September and the later period, defined by the first renesting attempt of a banded pair, lasted from 22 September through 10 November. Of 27 nesting attempts in the second half of the 1988 season, at least 14 were

by females that had bred successfully in the first half of the season. Of 37 banded birds that nested successfully in the first half of the breeding season (17 fully banded pairs, three partially banded pairs), 23 (62%) nested again in the second period.

Clutches laid in the initial period of the season ($\bar{x}$ = 7.3 ± 1.1 eggs, N = 27) were significantly larger (t = 2.2, df = 46, $P < 0.05$) than clutches laid in the later period ($\bar{x}$ = 6.7 ± 1.0 eggs, N = 21). There were no significant differences between the two periods in the number of young hatching (t = 0.6, df = 42, P = 0.6) or fledging (t = 0.3, df = 28, P = 0.8) per successful nest.

An average of 22.0 ± 9.2 days (range = 11–40 days, N = 10 pairs) elapsed from the fledging of the last chick at first nests until the laying of the first egg at second nests. This interval was positively correlated with the number of young fledged from the first nest (Spearman r = 0.62, $P <$ 0.05, N = 10), but was not correlated with the size of the first clutch (r = 0.23, $P > 0.10$, N = 10).

Pairbonds.—Pairs generally remained mated throughout the breeding season. Of 11 fully banded pairs that bred successfully in the first period and were resighted in the second period, 10 renested together (91%) and one changed mates (the female from this nest renested with a new mate).

Mate fidelity was more variable between breeding seasons. At least one member of 16 banded pairs that nested in 1988 nested again in 1989. Five members from these 16 pairs were resighted in 1989 with new partners, although in only two cases were the 1988 mates seen in 1989. Of the remaining 11 pairs from 1988, six remained together and nested in 1989; at least one member of the other five pairs nested in 1989 but with a partner who's identity could not be unequivocally confirmed due to partial band loss. In total, 37–69% of pairs remained mated for consecutive years and 31–63% changed mates between years.

Mate loss and replacement.—Three nesting attempts in 1988 were disrupted when one member of a pair disappeared or was found dead. The banded mate of one banded female disappeared after she had laid three eggs. The next day 12 males were present, displaying, vocalizing and fighting at her nest. The female discontinued laying but continued partial incubation for three days before abandoning the nest. Twelve days after ending incubation, this female initiated a new clutch with a new male. At another nest, containing six nestlings aged 10 to 19 days, the male disappeared. This female was pursued by four males and began to associate closely with one of them five days later. The new suitor followed the female to the nest and attempted to enter on many occasions, but the female always chased this new male away from the entrance. The female successfully raised six young. Predation might explain the disappearance of both of these parents; we witnessed an Aplomado Falcon (*Falco fe-*

moralis) flying with an adult parrotlet in its talons. At another nest, the female was found dead from unknown causes in the bottom of her nest box. The male stopped feeding his five nestlings (5–12 days old), and they died shortly thereafter.

Nest site fidelity.—Of the ten fully banded pairs that renested together in 1988, eight renested in the same cavity and two renested elsewhere. In addition, the female that switched mates renested in a new site, and the two banded birds that nested twice with unbanded birds renested in the same cavity. Therefore, 18 of 23 banded birds (78%) that nested twice, reused the same cavity.

However, holding possession of a nest site for a second attempt required a dedicated effort by the pair. After one or more young had fledged from a nest, other pairs, males, and groups of males began inspecting the cavity, perhaps anticipating its impending vacancy. Agonistic interactions occurred between the resident pair, intruding pairs, and other individuals. Parents displaced more intruders in this period than in any other period (egg laying: 0.47/h; incubation: 0.36/h; hatching: 0.17/h; nestling: 0.24/h; fledging: 1.0/h).

DISCUSSION

Green-rumped Parrotlets are highly aggressive towards conspecifics at nest sites. Agonistic behaviors observed in *F. passerinus* are common to many parrots (Brockway 1964b, Wyndham 1980, Skeate 1984, Snyder et al. 1987). High rates of nest box occupancy (Beissinger and Bucher 1991) and frequent interactions between pairs at nest sites suggests that breeding in *F. passerinus* may be limited by the availability of nest sites. In contrast, populations with an abundance of available nest sites exhibit agonistic behavior less often (Lanning and Shiflett 1983, Snyder et al. 1987), although agonistic behavior at nests was common for Budgerigars (Wyndham 1981) and White-tailed Black Cockatoos (*Calyptorhynchus funereus latirostris*) (Saunders 1982).

The head bowing, tail fanning and wing flicking courtship displays observed in *F. passerinus* are similar to those described for Puerto Rican Parrots (*Amazona vittata*) (Snyder et al. 1987), Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*) (Lanning and Shiflett 1983), White-tailed Black Cockatoos (Saunders 1974), White-fronted Amazons (*A. albifrons*) (Skeate 1984), Budgerigars (Brockway 1964a) and African parrots of the genus *Agapornis* (Dilger 1960). Snyder et al. (1987) suggested that head bowing is specifically related to pair formation in parrots and was seldom exhibited by established pairs of Puerto Rican Parrots. However, we observed this display in *F. passerinus* in all periods of the nesting cycle and during defense of nest areas from conspecifics. Thus, the display may help enhance, or reaffirm pair cohesion.

Nipping bouts occurred among pairs in *F. passerinus* especially during agonistic encounters with other pairs. This activity also appeared to reaffirm pair cohesion. Nipping bouts were observed in a different context in Puerto Rican Parrots as a highly aggressive activity between pairs (Snyder et al. 1987).

Bill clasping resembled a ritualized version of courtship feeding in which no food is actually transmitted. White-fronted Amazons exhibit a similar activity in which bills are gently locked while flicking tongues (Skeate 1984).

Allopreening and copulation bouts of Green-rumped Parrotlets were of long duration as described for other parrots. We saw male *F. passerinus* feeding females up to three weeks before the initiation of egg laying. Males began feeding females up to 26 days before initiation of egg laying in Puerto Rican Parrots (Snyder et al. 1987) and White-tailed Black Cockatoos (Saunders 1982), and fed females year-round in White-fronted Amazons (Skeate 1984) and *Agapornis* sp. (Dilger 1960). Allopreening, copulation and courtship feeding may serve to affirm pair cohesion.

Courtship feeding rates by male Green-rumped Parrotlets during egg laying were positively correlated with eventual clutch sizes laid by their mates (Fig. 4). Egg production by females may depend on the amount of nourishment they receive at this time (Dilger 1960, Nesbit 1977, Smith 1980). Alternatively, females may use male feeding rates as an honest indicator of paternal feeding in later stages of the nesting cycle (Smith 1980, Beissinger 1987). This may be particularly important in parrots because females do nearly all of the incubation and are almost completely dependent on males for food for long periods (Wyndham 1981, Saunders 1982, Skeate 1984, Snyder et al. 1987). Feeding rate was not correlated with clutch size during incubation, suggesting that males responded to the variable needs of their females.

The decision by females to switch from brooding to feeding young may be particularly difficult in parrots. Parrot nestlings are extremely altricial, growing and developing thermoregulatory capacity very slowly (Brockway 1964a, Bucher 1983). Because parrot broods typically are extremely asynchronous in hatching, the needs of the youngest nestlings to be brooded and of the oldest nestlings to be fed may conflict. Female Green-rumped Parrotlets shift their behavior from all day brooding to feeding nestlings when the oldest chick is about one to two weeks old (Figs. 3 and 5), a pattern also displayed in other parrots (Snyder et al. 1987, Saunders 1982, Stamps et al. 1985, Lanning and Shiflett 1983). This change in female behavior may occur quickly (Fig. 5), suggesting that nestling requirements change discretely. For example, nestlings may reach a stage when they no longer require brooding, or when the food demands of the brood reaches

a level that the male alone cannot fulfill. Especially in large broods, females may switch to feeding nestlings before the last hatched young can thermoregulate, when they are less than a week old. Unless they are incidentally brooded by older nestlings, last hatched chicks in large broods could possibly die of hypothermia on cool, rainy days, probably an unusual cause of mortality in tropical lowland birds (Skutch 1987).

Despite difficulties inherent in successfully raising a full brood, one *F. passerinus* female managed to fledge six young after her mate died. Puerto Rican Parrot (Snyder et al. 1987) and Budgerigar adults (Stamps et al. 1985) are also capable of rearing young alone. Widowed females of all three species began to choose a new mate immediately, even if he did not assist directly in raising her brood. The pairbond may be important to survival or for defending a nest from infanticide or replacement by other pairs, and may explain why females accept mates that do not appear to assist in feeding their young (Dilger 1960, Saunders 1974).

Although captive studies have noted that *Forpus* parrotlets are self-feeding at fledging (Mobbs 1981, Noble 1984), we occasionally saw fledglings fed by their parents up to 22 days after fledging. The duration of post-fledging care appears to be quite variable in parrots. Neither parent of wild Budgerigars was likely to feed young after fledging (Wyndham 1981) but in captivity young of this species did not become independent until two weeks after fledging (Brockway 1964b). After fledging, Thick-billed Parrots roamed in family groups and parents fed the young (Lanning and Shiflett 1983). Young White-tailed Black Cockatoos stayed with their parents until the next breeding season (Saunders 1982), while captive juvenile White-fronted Amazons did not feed themselves until 72 days after fledging (Skeate 1984). The extent of post-fledging care in parrots appears to be variable, and may depend in part on whether pairs can nest more than once during a breeding season and on the intensity of competition for nest sites in the population.

Inter-clutch intervals were not correlated with clutch size in *F. passerinus* or in Budgerigars (Stamps et al. 1985), but were correlated in both species with the number of young fledged. This suggests that either egg laying may not be as costly to females as rearing young, or that larger broods require longer periods of post-fledging care. Reproductive effort increased with brood size in Green-rumped Parrotlets, since feeding rates were positively related with the number of young in the nest.

Pair cohesion is very strong in most parrots (Dilger 1960, Brockway 1964a, Saunders 1974, Skeate 1984, Snyder et al. 1987). Aviculturalists have reported that pairs of Green-rumped Parrotlets mate for life and that females often kill new males that are placed in their cages (Noble 1984). In our population, most pairs remained mated throughout the

breeding season, but fewer pairs remained mated between years. Mate switching has also been recorded in Puerto Rican Parrots (Snyder et al. 1987), but not in White-tailed Black Cockatoos (Saunders 1974, 1982).

In conclusion, parrot reproduction is characterized by a long incubation period, a high degree of hatching asynchrony, very altricial nestlings, and slow growth of young. These characteristics may have resulted in the extreme division of parental care roles that parrots exhibit for much of the breeding cycle. Females depend on males to feed them and their young for prolonged periods and must develop confidence that their mates will not desert them (Beissinger 1987). Furthermore, in populations with a shortage of available nest sites, a high degree of intraspecific aggression and competition for nest sites may result in coordination of activities by members of a pair to protect their nest site. These factors may require a high degree of cooperation between mates and may account for the high degree of pair cohesion in many parrot species.

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DENSITY-INDEPENDENT FACTORS AFFECTING THE AVIAN DIVERSITY OF THE TALLGRASS PRAIRIE COMMUNITY

JOHN L. ZIMMERMAN[1]

ABSTRACT.—The low species richness in grassland bird communities has been hypothesized to result from competition in a simplistic, saturated habitat (Cody) or to result from the periodic occurrence of climatic extremes that prevent drought-susceptible species from perennial settlement (Wiens). Predictions based on these two hypotheses were evaluated using June population estimates on burned and unburned tallgrass prairie over the decade, 1981–1990, on the Konza Prairie Research Natural Area, Kansas. The results of these analyses support the notion that drought tolerance is the primary factor that determines membership in the tallgrass prairie community. When drought and fire are coincidental, however, the community does respond in a manner commensurate with the saturation hypothesis by a reduction in bird abundances but not a decrease in species richness. *Received 9 May 1991, accepted 10 Sept. 1991.*

The avian community of the North American tallgrass prairie, like those of grasslands throughout the world, is not diverse, less than ten species being the norm (Cody 1966). Furthermore, the number of breeding species is not only small but relatively constant (Wiens 1973). While "the species occupying these grasslands are optimally adapted to present environmental conditions and are comprised of the best selection of the species potentially available for habitat occupancy" (Cody 1968:136), there is disagreement as to the definitive factors that provide this "best selection."

Cody (1966, 1968) considers these communities to be saturated, with the component species having divided up the limited resources available in the single-stratum vegetative substrate to the degree that there is no opportunity for exploitation by any additional species. Knopf et al. (1990) have suggested that birds inhabiting grassland-shrubsteppe use the vigor of the vegetation as a critical predictor of food availability, implying that food availability is an important dimension of their niches. This suggests to me, at least, that food is limiting and that competition does affect the structure of the community.

Wiens (1974), on the other hand, notes that the participation of birds in grassland ecosystem energy flow is minuscule (1.0–2.5 kcal/m^2 per season) and that there is no resource partitioning (Rotenberry and Wiens 1980), concluding that grassland communities are not saturated and hence competition cannot explain the low species richness. Rather, his analysis

[1] Div. Biology, Ackert Hall, Kansas State Univ., Manhattan, Kansas 66506.

suggests that the paucity of grassland species results from periodic climatic extremes which, acting like a bottleneck, have permitted only a few species to survive and be successful during those times of environmental stress. As evidenced by the considerable annual variation in grassland bird densities (Wiens and Dyer 1975), populations then blossom during the intervening benign periods of more than adequate resources. Ricklefs (1987) also considers competition and niche theory to be inadequate in explaining local community diversity, since this notion excludes the effects of regional and evolutionary history as well as the impact of unique events and circumstances.

As part of the continuing NSF-supported Long-term Ecological Research effort at The Nature Conservancy's 3500-ha Konza Prairie Research Natural Area in Riley and Geary counties, Kansas, grassland bird populations have been measured during June for the past decade. Fire, imposed on watershed-sized areas at intervals from annually to every 20 years, is a major aspect of the experimental and management plan at Konza Prairie and provides a mechanism to investigate these contrasting explanations for grassland bird species diversity.

METHODS

During the first two weeks of June from 1981 through 1990, variable distance transects (Burnham et al. 1980) were completed over a distance of 1.58 km in burned prairie and from 3.27 to 6.83 km in unburned prairie on a set of permanently marked routes. The transects in burned prairie were located in two watersheds that had been burned in early April every year since either 1972 or 1978 and continued to be annually burned throughout the course of this study. The unburned transects were in seven watersheds that had not been burned since at least 1971, although 2.6 km of the total transect length had been affected by a wildfire in late April 1980. During the course of the study, however, no fires occurred, although total transect length had to be decreased as certain of the watersheds were shifted to other burning treatments in 1988 and 1989.

Although perpendicular distances of bird sightings are available in the data sets, numbers of records were insufficient to provide absolute density values for individual species. These data do provide annual, but unreplicated, measures of species richness and relative abundances in birds/km. Species seen only once in this decade were excluded from this analysis as were raptors, swallows, and the lekking Greater Prairie-Chickens (*Tympanuchus cupido*), taxa that are not adequately quantified by this method. While comparisons based on single-year censuses at different locations should be approached with skepticism (Wiens 1981), there are situations, such as annually repeated observations at the same locations, for which this approach is satisfactory (Kantrud 1981).

Precipitation data have been collected continuously on site since 1983. March soil moisture has been shown by Briggs and Knapp (pers. comm.) to be the best predictor of above-ground primary productivity, and these values were obtained at a depth of 25 cm with neutron probes and are based on a mean of two tubes per watershed and averaged across seven watersheds. Soil moisture data have been collected only since 1984.

Species recorded on unburned prairie were divided into core-species (recorded in all years) and erratics (recorded between 20% and 90% of the years). This restrictive definition for

core-species was purposefully conservative so that any ambiguity resulting from the actual absence of a species or its apparent absence because of the limitations of the methodology would be circumvented, although it has been my experience that over these transect distances species that were present during a particular breeding season were seldom missed on the June transect. The core-species, in turn, were divided into those dependent on grassland habitats and those requiring significant presence of woody vegetation. The Brown-headed Cowbird (*Molothrus ater*), a core species, parasitizes hosts in all habitats and is classified as habitat independent. These same assignments were used for birds in burned prairie, although many of the core species were not perennial in that habitat.

RESULTS AND DISCUSSION

As is to be expected (see Risser et al. 1981), the diversity among the grass-dependent species is low, and most species (71%) are present only during the breeding season. Of these summer residents, 60% winter within the north temperate zone while the remainder winter in the neotropics or south temperate zone (Table 1, A.O.U. 1983).

Are grassland bird communities saturated?—Unburned prairie is spatially heterogeneous, presenting a mosaic of standing dead vegetation, C3 and C4 grasses, forbs, and woody vegetation. Annually burned prairie is more homogeneous, being floristically and structurally simple, since fire eliminates standing dead vegetation and ground litter and reduces coverage by C3 grasses, forbs, and woody vegetation (Gibson 1989). Thus fire results in a reduction in plant species richness. Fire also reduces evenness in the plant community by encouraging the dominance of the warm-season (C4) grasses, primarily big bluestem (*Andropogon gerardii*) (Collins and Gibson 1990). Fire also increases subsequent primary productivity (Knapp and Seastedt 1986), increasing energy resources available to consumer species (Evans 1988).

If grassland bird communities are saturated within limits imposed by the simplicity of the vegetative substrate, fire should reduce the number of bird species even more by further simplifying the vegetative structure of the community, yet increase the abundances of the remaining species by augmentating the energy resource base. When all species were considered (Table 2), there was a significant decrease in species richness with burning (Student's $t = 12.50$, $df = 18$, $P < 0.01$). This results primarily from the low coverage of woody vegetation on burned prairie and its unsuitability to woody-dependent core-species and most erratics. If just the grass-dependent core-species were considered, there was also a significant decrease in species richness (Student's $t = 11.36$, $df = 18$, $P < 0.01$). This latter result accrues from the preemptive impact of removal of litter and standing dead on Henslow's Sparrows (*Ammodramus henslowii*) (Zimmerman 1988) and the virtual elimination of Common Yellowthroats (*Geothlypis trichas*) on burned prairie, which is probably also

Table 1

Mean (±SE) Relative Abundances (Birds/km) of Species Recorded from 1981 through 1990 on Transects in Unburned and Burned Tallgrass Prairie on the Konza Prairie Research Natural Area, Kansas. (Raptors, Prairie-chickens, Swallows Excluded)

	Unburned	Burned
Core-species, present every year		
Grass-dependent species		
Ring-necked Pheasant, *Phasianus colchicus*	1.0 ± 0.16	0.2 ± 0.10[a]
Upland Sandpiper, *Bartramica longicauda*	2.9 ± 0.46	5.2 ± 0.70
Mourning Dove, *Zenaida macroura*	4.0 ± 0.39	2.2 ± 0.45
Common Yellowthroat, *Geothlypis trichas*	3.1 ± 0.39	0.2 ± 0.17[a]
Dickcissel, *Spiza americana*	13.9 ± 0.90	12.3 ± 1.86
Grasshopper Sparrow, *Ammodramus savannarum*	8.3 ± 0.67	6.8 ± 0.90
Henslow's Sparrow, *A. henslowii*	2.8 ± 0.59	0
Red-winged Blackbird, *Agelaius phoeniceus*	1.6 ± 0.22	3.8 ± 0.37
Eastern Meadowlark, *Sturnella magna*	8.0 ± 0.41	6.8 ± 0.80
Woody-dependent species		
Northern Bobwhite, *Colinus virginianus*	3.0 ± 0.47	1.2 ± 0.44[a]
Eastern Kingbird, *Tyrannus tyrannus*	1.4 ± 0.18	1.5 ± 0.19
House Wren, *Troglodytes aedon*	1.3 ± 0.29	0
Brown Thrasher, *Toxostoma rufum*	2.8 ± 0.23	0.7 ± 0.18[a]
Bell's Vireo, *Vireo bellii*	2.3 ± 0.52	0
Field Sparrow, *Spizella pusilla*	2.8 ± 0.45	0
Northern Oriole, *Icterus galbula*	0.4 ± 0.09	0.3 ± 0.10[a]
American Goldfinch, *Carduelis tristis*	2.3 ± 0.55	0
Habitat-independent species		
Brown-headed Cowbird, *Molothrus ater*	8.4 ± 0.51	6.1 ± 1.24
Erratic species, present 20–90% of years		
Grass-dependent species		
Killdeer, *Charadrius vociferus*	0.4 ± 0.03	0
Common Nighthawk, *Chordeiles minor*	0.3 ± 0.10	1.0 ± 0.36
Lark Sparrow, *Chondestes grammacus*	0.1 ± 0.03	0
Woody-dependent species		
Yellow-billed Cuckoo, *Coccyzus americanus*	0.6 ± 0.13	0
Red-headed Woodpecker, *Melanerpes erythrocephalus*	0.3 ± 0.06	0
Red-bellied Woodpecker, *M. carolinus*	0.1 ± 0.05	0
Northern Flicker, *Colaptes auratus*	0.7 ± 0.15	0.2 ± 0.10
Eastern Phoebe, *Sayornis phoebe*	0.1 ± 0.07	0
Great Crested Flycatcher, *Myiarchus crinitus*	0.2 ± 0.06	0
Blue Jay, *Cyanocitta cristata*	0.3 ± 0.08	0
Black-capped Chickadee, *Parus atricapillus*	0.1 ± 0.05	0
Tufted Titmouse, *P. bicolor*	0.1 ± 0.04	0
Eastern Bluebird, *Sialia sialis*	0.4 ± 0.24	0

TABLE 1
CONTINUED

	Unburned	Burned
American Robin, *Turdus migratorius*	0.2 ± 0.05	0.1 ± 0.08
Gray Catbird, *Dumetella carolinensis*	0.2 ± 0.08	0
Loggerhead Shrike, *Lanius ludovicianus*	0.2 ± 0.15	0
European Starling, *Sturnus vulgaris*	0.3 ± 0.12	0
Warbling Vireo, *Vireo gilvus*	0.1 ± 0.03	0
Yellow Warbler, *Dendroica petechia*	0.1 ± 0.03	0
Northern Cardinal, *Cardinalis cardinalis*	0.3 ± 0.10	0
Blue Grosbeak, *Guiraca caerulea*	0.1 ± 0.05	0
Rufous-sided Towhee, *Pipilo erythrophthalmus*	0.6 ± 0.56	0
Common Grackle, *Quiscalus quiscula*	0.1 ± 0.02	0.8 ± 0.28
Orchard Oriole, *Icterus spurius*	0.1 ± 0.09	0

[a] Present less than every year in burned prairie.

a result of the loss of litter. While both of these responses are in the direction predicted by the saturation hypothesis, the reductions are not due to competitive exclusion. Rather they are due to the eradication of critical niche dimensions by the alteration of the physical structure of the habitats.

Relative abundances were not modified in the expected direction, significantly decreasing rather than increasing when all species were considered (Student's $t = 4.46$, $df = 18$, $P < 0.01$) and not changing when just the grass-dependent core-species (exclusive of Henslow's Sparrows and Common Yellowthroats) were compared (Student's $t = 0.60$, $df = 18$, $P > 0.05$). The former results from the elimination of so many core and erratic species dependent upon woody vegetation. The absence of a difference in relative abundances of the grass-dependent core-species common to both treatments suggests that these populations are not at resource-imposed saturation levels, that indeed, the resource base of this bird community is not actually critical. Food resources are sufficient in unburned prairie, and the increases in both primary production and primary consumer populations in response to burning have no effect on the numbers of birds in the community. Indeed, resources appear sufficient, if not even superabundant.

Does a climatic bottleneck select species in the grassland bird community?—Precipitation is the variable that imposes the characteristic life form to grasslands from the mesic tallgrass prairie on the eastern edge of the rainshadow of the Rocky Mountains to the xeric short-grass plains that ascend to the foothills and spill over into the inter-mountain parks. Furthermore, precipitation is highly variable; abnormally wet or dry years

TABLE 2

ANNUAL SPECIES RICHNESS AND TOTAL RELATIVE ABUNDANCE (BIRDS/KM) IN BURNED AND UNBURNED TALLGRASS PRAIRIE

Year	All species[a]		Grass core-species		Woody core and erratic species	
	No.	Birds/km	No.	Birds/km	No.	Birds/km
Unburned prairie						
1981	26	52.4	9	34.1	16	11.0
1982	32	57.3	9	36.2	22	14.1
1983	35	69.2	9	44.1	25	18.5
1984	31	84.1	9	50.0	21	24.8
1985	34	76.8	9	47.2	24	21.0
1986	32	89.2	9	56.5	22	23.3
1987	33	98.5	9	54.0	23	33.5
1988	26	82.0	9	46.4	16	25.0
1989	23	71.6	9	45.9	13	19.9
1990	26	75.6	9	41.6	16	25.7
Mean	29.8	75.7	9	45.6[b]	19.8	21.7
SE	1.32	4.41	0	2.24	1.32	2.01
Burned prairie						
1981	12	48.7	6	38.6	5	5.7
1982	10	33.4	6	27.2	3	2.5
1983	10	44.3	7	32.3	2	1.9
1984	11	44.3	6	34.2	4	5.7
1985	11	41.8	6	34.8	4	3.2
1986	12	46.8	6	38.6	5	6.3
1987	14	74.7	8	55.1	5	7.0
1988	13	58.2	7	37.3	5	8.9
1989	15	41.8	7	27.8	7	9.5
1990	13	62.0	6	50.6	6	8.2
Mean	12.1	49.6	6.5	37.6	4.6	5.9
SE	0.53	3.81	0.22	2.84	0.40	0.75

[a] Includes Brown-headed Cowbird, hence is greater than the sum of the other two categories.

[b] This mean reduced to 39.7 for comparison with burned value by excluding totals for Henslow's Sparrow and Common Yellowthroat.

occur in tallgrass prairie about once every four years (Wiens 1974). If bird populations are affected by precipitation, there should be a correlation between their numbers and the amount of moisture available. The analysis of product-moment coefficients for a number of ways of expressing this variable on an annual basis correlated with the total relative abundances of birds per year in unburned and burned prairie revealed that March soil moisture is the only variable that was significantly correlated with both unburned ($r = 0.77$, $N = 7$, $P < 0.05$) and burned ($r = 0.80$, $N = 7$, $P < 0.05$) grassland bird numbers (Table 3).

TABLE 3
PEARSON PRODUCT-MOMENT CORRELATION COEFFICIENTS BETWEEN BIRDS/KM AND THE FOLLOWING VARIABLES

	Unburned	Burned
March soil moisture	0.77[a]	0.80[a]
Previous year's precipitation	0.81[a]	0.39
Current year's precipitation	0.31	−0.30
Current March–June precipitation	0.34	−0.20

[a] $P < 0.05$.

The saturation hypothesis was not supported by the effects of burning on species richness and relative abundance, but moisture availability provides a mechanism to not only again test that hypothesis, but the bottleneck hypothesis as well. If the saturation hypothesis for grass-dependent core-species is true, there should be a positive correlation between abundances and soil moisture, since soil moisture is positively correlated with aboveground productivity and hence a more structurally complex and energetically richer habitat. If the bottleneck hypothesis is true, however, there should be no correlation between the relative abundances of the grass-dependent core-species and soil moisture, since these species are present because they have been affected by previous selective impacts of climatic extremes. These species tolerate these extremes, and March soil moisture, for example, should be irrelevant to their abundance.

The woody-dependent core-species as well as the erratics are not grassland species in the strict sense (see Mengel 1970), but have invaded the tallgrass prairie through the forest-prairie mosaic to the east. Thus they have not been influenced in their evolution by the assumed bottleneck of climatic extremes. As a control comparison, the relative abundances of these two species groups have been combined and similarly related to March soil moisture. In habitats where periodic aridity is not a characteristic of the environment, drought does markedly decrease breeding densities (Smith 1982). I expected, therefore, that these numbers should be positively correlated with soil moisture.

When this analysis was completed for populations on unburned prairie, the results support the bottleneck hypothesis. The correlation for the grass-dependent core-species was not significant ($r = 0.40$), whereas that for the woody-dependent core-species and erratics was positive and significant ($r = 0.86$, $N = 7$, $P < 0.01$). When the same analysis was done for burned prairie, however, the relationships were reversed. The numbers of grass-dependent core-species were significantly correlated with March

soil moisture ($r = 0.94$, $N = 7$, $P < 0.01$), but those of the woody-dependent core-species and erratics were not ($r = 0.10$).

The lack of significance for this latter group is arithmetic. Their abundances are so low in burned prairie (Table 2) that they do not generate the necessary differences in products that are part of the computation. The interesting question, of course, is why there is a significant correlation of the relative abundances of the grass-dependent core-species with soil moisture in burned prairie, even though the bottleneck hypothesis predicts that this relationship should not exist, as it did not in unburned prairie.

I suggest that in the tallgrass prairie, the appropriate species are indeed few because they are the hardy few that can withstand the periodic occurrence of climatic severity, and their populations are not affected by these extremes as long as the structural complexity of the habitat has not fallen below some threshold level. In normal and wet years, above-ground plant biomass is usually greater on burned prairie than it is on unburned prairie (Hulbert 1988), but in drought years the primary productivity of burned prairie drops below that of unburned prairie (Briggs et al. 1989). Fire induces a reduction in the structural complexity of the prairie, but on average, this change does not significantly depress relative abundances among the grass-dependent core-species when moisture is sufficient. When drought inhibits the above-ground productivity of burned prairie to a level below an acceptable threshold, however, fire does affect these bird populations.

The controversy regarding the factors that affect bird diversity in grasslands appears to be a function of whether the biotic factors (vegetative structure and food resources) result in saturation and the ensuing interspecific competition involved in their utilization determines species richness or whether it is the abiotic factors (climatic instability) that select for a set of "bottleneck-tolerant" species without the operation of competition. My analysis suggests that adaptation to periodic drought imposes the primary requirement for membership by the grass-dependent core-species in the tallgrass prairie community. The low species richness reflects the reality that few species have this ability. Since the North American grassland biome is a relatively young assemblage of species, perhaps few species actually have had the time to evolve this tolerance (F. Knopf, pers. comm.). Fire has a direct structural impact on the community and eliminates certain species by affecting critical dimensions of their niches, not as a result of competitive resource partitioning, but rather by obliterating species-appropriate resource space. In average and wet years, fire does not increase bird abundance concomitant with an increase in trophic resources as would be expected if the community were saturated. When drought is coupled with periodic fire, however, the community does reach

a state of biotic saturation so that even these drought-adapted species suffer a decrease in abundance, although no species drops out entirely from the community. Wiens (1974) had speculated that this could occur.

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NESTING ECOLOGY OF THE LOGGERHEAD SHRIKE IN SOUTHWESTERN OKLAHOMA

JACK D. TYLER[1]

ABSTRACT.—Loggerhead Shrike (*Lanius ludovicianus*) nests were studied in southwestern Oklahoma from 1985 through 1988. Pairing began in late February to early March, and completed nests were found from 13 March to 20 June. Nesting peaked in mid-April, with second nestings from late May to late June. Average length of the nesting season was 11 weeks. Almost one-third of all nests were built in Osage orange (*Maclura pomifera*) trees, but netleaf hackberry (*Celtis reticulata*), Chinese elm (*Ulmus pumila*), and eastern red cedar (*Juniperus virginiana*) were also used frequently. Mean nest height was 3 m, and average clutch size was 5.8. At least one egg hatched in 84% of clutches. A mean of 16.9 days was required for incubation and the average fledging period was 16.8 days. Probability of survival using Mayfield's (1961, 1975) method was 46%. *Received 30 July 1990, accepted 15 Sept. 1991.*

National Audubon Society Christmas Bird Counts and United States Fish and Wildlife Service (USFWS) Breeding Bird Surveys indicate that the Loggerhead Shrike (*Lanius ludovicianus*) has been extirpated or is rare throughout much of the eastern United States. It has been on the *American Birds* Blue List since 1971 (Arbib 1971, Tate 1986), and a status survey is being conducted by the USFWS. Possible explanations usually suggested for the shrike's decline are pesticides (Erdman 1970, Anderson and Duzan 1978, Kridelbaugh 1981, Phillips 1986), loss of nesting habitat (Graber et al. 1973), and intensive farming practices (Kridelbaugh 1982). The shrike is still common in Oklahoma (Droege and Sauer 1990). However, its numbers continue to decline at the rate of about 5% a year along fully 75% of the Oklahoma routes where it has been detected (USFWS, unpubl. data). There is little information available on the breeding ecology of the Loggerhead Shrike in the southern Great Plains. The present four-year study was undertaken in the spring of 1985 with the objective of contributing basic reproductive data from this part of the species' range.

STUDY AREA

The study area was within a 24-km radius of Lawton, Comanche County, southwestern Oklahoma, in the mixed-grass plains biotic district of Blair and Hubbell (1938). Most area soils have been derived from the underlying Permian redbeds. Average elevation is approximately 350 m. Pasturelands interspersed with cultivated fields predominated, many of the former covered more or less by mesquite (*Prosopis juliflora*) or scattered small trees of various kinds. Occasional farmstead plantings and Osage orange (*Maclura pomifera*) hedgerows were common. The level to gently rolling terrain was dotted with numerous

[1] G. M. Sutton Avian Research Center, P.O. Box 2007, Bartlesville, Oklahoma 74005-2007.

stockponds and irregularly dissected by intermittent streams. Many of these were bordered by riparian woodlands and the largest, East Cache Creek, bisected the research area. Ranching was the primary local enterprise, with winter wheat, hay, and cotton the major crops.

The climate is of the temperate continental type, with great fluctuations in both moisture and temperature from year to year. Rapid weather changes are common. Precipitation in Lawton averages about 80 cm per year, and the mean January and July temperatures, respectively, are 4.6 and 27.5°C.

METHODS

When shrikes started to pair in late winter and early spring, former nest sites and other localities in suitable habitat were visited every two or three days until nest construction had begun or the site was abandoned. Thereafter, nests were checked at three- to six-day intervals until time of hatching or fledging neared, when more frequent visits were made. Data for 109 nests (28 in 1985, 27 in 1986, 26 in 1987, and 28 in 1988) were pooled so that probability of survival from onset of incubation to fledging could be calculated using Mayfield's (1961, 1975) exposure-day method. For nests that contained full clutches, or that fledged young, but for which the exact number of days of incubation or days as nestlings was not available, known averages from other nests found the same year were used. The probabilities of nest survival during the hatching period (two days) and during the nestling period were also determined. The known average nestling period for each year was assigned to other nests that fledged young that year, but for which exact data were not available (7, 11, 7, and 10 nests, respectively, by year).

RESULTS

Twenty-three species of dense woody plants, most less than 6 m tall and usually isolated or in hedgerows, were selected as nest sites. Placement of nests frequently varied from year to year in a given territory but were usually within 100 m of the previous year's nest. The mean height for 128 nests was 2.97 ± 0.16 m. The principal trees used for nesting in southwest Oklahoma and the average percent of total nests contained in each were: Osage orange (31), hackberry (*Celtis reticulata*) (13), Chinese elm (*Ulmus pumila*) (11), and eastern red cedar (*Juniperus virginiana*) (9). Seven other woody plants contained from 3.0% to 5.5% of all nests, and 12 additional species held nests only once (Table 1).

During the four nesting seasons from 1985 to 1988, 133 nesting pairs were located. The nesting season, from initial nest construction until the last fledglings could fend for themselves, lasted about 12 weeks in 1985, 10 in 1986, 9 in 1987, and 13 in 1988. The overall average was 11 ± 1.8 weeks.

Pairing began from late February to mid-March, as winter territories broke down and some birds began to arrive from the south. Extreme dates for first evidence of nest construction during the study were February 23 and March 15, and the earliest egg was discovered on March 13. Peak nesting occurred about the first week of April (Fig. 1), and by May 2, 78 of 88 nests (89%) held complete clutches. A smaller second period of

TABLE 1

SPECIES OF TREES AND SHRUBS IN WHICH 133 SHRIKE NESTS WERE BUILT IN SOUTHWESTERN OKLAHOMA, 1985–1988

	1985		1986		1987		1988		Total no.	Overall avg.
	No.	%	No.	%	No.	%	No.	%		
Osage orange (*Maclura pomifera*)	8	22.0	7	22.6	13	42.0	13	36.1	41	30.7%
Hackberry (*Celtis reticulata*)	6	17.0	5	16.0	3	9.7	3	8.3	17	12.8%
Chinese elm (*Ulmus pumila*)	6	17.0	5	16.0	2	6.4	2	5.5	15	11.2%
Red cedar (*Juniperus virginiana*)	4	11.0	2	6.4	4	12.9	2	5.5	12	9.0%
Mulberry (*Morus* sp.)	4	11.0	—	—	—	—	4	11.1	8	5.5%
American elm (*Ulmus americana*)	1	2.9	2	6.4	2	6.4	1	2.8	6	4.6%
Chittamwood (*Bumelia lanuginosa*)	1	2.8	—	—	4	12.9	1	2.8	6	4.6%
Cottonwood (*Populus deltoides*)	—	—	2	6.4	—	—	1	2.8	3	4.6%
Black willow (*Salix nigra*)	3	8.0	3	9.7	—	—	—	—	6	4.4%
Black locust (*Robinia pseudo-acacia*)	—	—	1	3.2	1	3.2	2	5.5	4	2.9%
Hawthorne (*Crataegus* sp.)[a]	2	5.5	1	3.2	1	3.2	—	—	4	2.9%

[a] Plus 12 other species used only once.

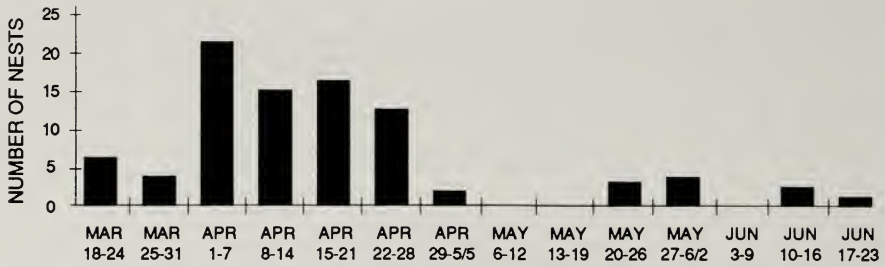

FIG. 1. Dates that 88 shrike nests were completed in Oklahoma, 1985–1988.

breeding activity took place between May 21 and June 20, when clutches in the remaining 10 nests were filled. Most of these were second broods, however, and there was no "peak." Dates for the last egg of the final clutch each year were June 18, 1, 10, and May 31; the average date was June 8.

First eggs for each of the four respective years were deposited on March 20, 13, 30, and 26. Earliest completed clutches were recorded on March 21, March 18, April 4, and March 31. Dates of first hatching were April 6, 3, 19, and 16.

Table 2 summarizes reproductive success for all four years. At least one egg hatched in 92% of all nests that contained eggs in 1985. This increased to 95% in 1986, fell to 69% in 1987, and rose to 81% in 1988 (Table 2). The overall mean percentage was 84%. The percentage of 133 nests fledging at least one young, although only 46% in both 1985 and 1987, was 63% in 1988 and 83% in 1986. The four-year average was 60%.

Clutch size ranged from three to seven eggs and averaged 5.8 for 101 nests. The mean was 5.7 in 1985, 5.6 in 1986, and 5.9 in 1987 and 1988.

The length of incubation (penultimate egg = day one) ranged from 16.6 days in 1988 to 17.1 in 1985. The four-year mean among 55 nests was 16.9 days. For nestlings in 28 nests with data, the average time from hatching to fledging was 16.8 days.

Ten of 37 pairs (27%) studied in 1985 attempted second broods, nine of 28 pairs (32%) in 1986, only two among 26 pairs (7.7%) did so in 1987, and three of 31 pairs (9.7%) in 1988. The overall average for all pairs was 19.1%. At one location, shrikes built second nests during the first three years only. At two nest sites, the same pair renested every year except 1987, and in 1986 one pair of birds incubated eggs in three successive nests. Second clutches were initiated from mid-April to mid-June. Out of 18 eggs laid in second nests, a maximum of three young fledged. Only three nesting territories were used all four years.

Nineteen of 109 nests failed while being exposed for 1663 days during

TABLE 2

REPRODUCTIVE SUCCESS OF LOGGERHEAD SHRIKES IN SOUTHWESTERN OKLAHOMA, 1985–1988

	Clutch size		Incubation period (days)		Hatching success[a]		Nestling period (days)		Fledging success[b]		Attempted second broods	
Year	N	$\bar{x} \pm SD$	N	$\bar{x} \pm SD$	N	%	N	$\bar{x} \pm SD$	N	%	Pairs	%
1985	28	5.7 ± 0.86	8	17.1 ± 0.66	37	92	2	15.5 ± 2.00	41	46	37	27.0
1986	24	5.6 ± 0.88	15	16.9 ± 0.26	38	95	3	17.3 ± 0.71	35	83	28	32.0
1987	24	5.9 ± 0.62	19	16.9 ± 0.75	26	69	8	17.1 ± 2.10	26	46	26	7.7
1988	24	5.9 ± 0.29	13	16.6 ± 0.76	32	81	15	17.3 ± 1.54	32	63	31	9.7

[a] At least one egg hatched.
[b] At least one young fledged.

incubation for a daily mortality rate of 1.1% per nest-day. Daily nest survival rate was therefore 98.9%. Predation was suspected to have caused the failure of 10 nests, six were deserted, and three others were destroyed by high winds. Because the average incubation period for 55 nests was 16.9 days, successive survival rate was calculated for each day of incubation (98.9^{17}). Thus, the number of nests expected to remain if 1.1% of 109 nests were lost daily for 17 days was 94 (93.9%).

The hatching period in shrikes in normally two days, but the date that the first egg began to hatch was considered the final day of incubation for that nest. Only 468 of 619 eggs present at hatching time produced nestlings within two days of the onset of hatching, giving a probability of survival during the hatching period of 76%.

Of 90 nests observed during the nestling period, 27 failed during 1308 days of exposure, for a mortality rate of 2.1%. Therefore, the daily survival rate for nestlings was 97.9%. Because 16.8 days (rounded to 17) are required on average before nestlings leave the nest, the overall nestling survival rate was 64% (97.9^{17}).

Probability of survival of any nest from the start of incubation until the young had fledged was then computed: $0.94 \times 0.76 \times 0.64 = 0.46$, or 46%. Therefore, of 109 nests in which incubation was begun, the probability that any one would fledge at least one young bird was 46%.

DISCUSSION

The average nest height in southwestern Oklahoma (N = 128) was 2.97 ± 0.16 m. In Missouri and Alabama, the average was slightly higher, 3.2 m (Kridelbaugh 1983) and 3 m (Siegel 1980), respectively, but in Colorado (Porter et al. 1975) it was only 2 m. Graber et al. (1973) also found that 88% of shrike nests were built in Osage oranges in northern and central Illinois, and in Kansas, too, this species was used for nesting more than any other (Johnston 1964). However, red cedar held the largest percentage of nests in Missouri (Kridelbaugh 1983), Alabama (Siegel 1980), Virginia (Luukkonen 1987), and South Carolina (Gawlik and Bildstein 1990). In Colorado, Porter et al. (1975) found that elms, willows (*Salix* sp.), cottonwoods (*Populus* sp.) and Russian olive (*Elaeaganus angustifolia*) supported 70% of all shrike nests.

As in Oklahoma, shrikes in Missouri (Kridelbaugh 1983) began to arrive and set up breeding territories during mid-February, and the earliest completed nest was found there on March 23, compared to March 13 in Oklahoma. The earliest active nest in South Carolina was discovered on 17 March (Gawlik and Bildstein 1990). Egg-laying was not initiated in Colorado until the first week in May (Porter et al. 1975). Peak nesting activity in Missouri and Illinois (Kridelbaugh 1983, Graber et al. 1973)

was in late April, with a second peak in late May in Missouri. Height of breeding in Alabama was in early April (Siegel 1980), as was the case in Oklahoma (Fig. 1). Porter et al. (1975), however, reported most nesting during late May in the higher latitudes of Colorado.

Hatching success for all years in Oklahoma varied from 69% in 1987 to 95% in 1986, averaging 81% (Table 2). Hatching at most Oklahoma nests took place around the first week of May. During the two years that success was highest (1985, 1986), April was exceptionally wet. The converse was true in 1987 and 1988, and hatching success was not as high. In 1988, when precipitation was only slightly below average but evenly distributed, success was greater than in 1987. However, only 2.0 mm of rain fell in April 1987, versus the norm of 63.5 mm (U.S. Weather Service, Fort Sill, Oklahoma). The two years of highest hatching success were also those with the greatest number of second nesting attempts (Table 2). This 81% average hatch success in Oklahoma is very close to the 79.5% found in Colorado (Porter et al. 1975). For 43 Missouri nests during two years, Kridelbaugh (1983) reported a mean of 85%.

For all four years, an average 60% of all nests fledged at least one young bird. The range was 46% to 83%. A majority of young shrikes fledged during mid to late May in Oklahoma. Poor success in both 1985 and 1987 was probably attributable to inclement weather. Heavy rains, high winds, and low temperatures in April 1985 were followed by inordinate dryness in May and local flooding in early June. In 1987, on the other hand, April was a month of extreme drought. The pendulum swung to the other extreme again during the last two weeks of May, when 279 mm of rain fell, 203 mm of it within one 96-h period (U.S. Weather Service, Fort Sill, Oklahoma). During this deluge, one to four nestlings were lost from five different nests. The Oklahoma mean of 60% is in close agreement with Kridelbaugh's (1983) of 59.4% for 43 nests in Missouri. The figures from Alabama (50%) and Colorado (55.9%) were somewhat lower (Siegel 1980, Porter et al. 1975).

For 101 Oklahoma nests, the average clutch size was 5.8. During the first two years of the study, in which both hatching success and attempts at second broods were at their highest levels, clutch size averaged 5.6 and 5.7, respectively, whereas the mean size during the other two years was 5.9 (Table 2). This overall Oklahoma average of 5.8 was the same as that for 34 nests in Minnesota (Temple and Brooks 1986). It ranged from 5.1 (N = 57) in Virginia (Luukkonen 1987) to 6.4 (N = 65) for Colorado (Porter et al. 1975) and is very near the 5.7 average found in both Missouri (N = 55) and Illinois (N = 134) (Kridelbaugh 1983, Graber et al. 1973). The mean clutch size of 32 Kansas nests, however, was only 5.3 (Johnston 1964).

The mean incubation period for Oklahoma shrikes was 16.9 days among 55 nests, which corresponds to Lohrer's (1974) average for 16 nests in Florida, and is almost identical to that for Missouri, where Kridelbaugh (1983) found it to be 17 days for 13 nests. For 14 California nests, this average was 16 days, as it was in Colorado (Miller 1931, Porter et al. 1975).

At 28 nests in Oklahoma, the nestling period averaged 16.8 days. Similarly, it averaged 17.6 days in Alabama and 17 for both Colorado and Florida (Siegel 1980, Porter et al. 1975, Lohrer 1974). This figure was 19 days for 14 Missouri nests (Kridelbaugh 1983) and 20 in California (Miller 1931).

In Oklahoma, the percentage of shrike pairs that attempted two broods ranged from 7.7% in 1987 to 32% in 1986. The average was 19.1%. As seen in Table 2, during the first two years, when hatching success was greatest, more renestings took place, and vice versa. The very low renesting rate of 7.7% in 1987 was probably due to a 279-mm rainfall in late May. Conversely, a severe drought gripped the area during this same period in 1988, which might have accounted for the low number of second nestings that year (U.S. Weather Service, Fort Sill, Oklahoma). In Missouri, Kridelbaugh (1983) found that 22% of birds he studied renested in 1980 and 1981. Fifteen (58%) of 24 second nestings in Oklahoma succeeded, a higher percentage than the 46% overall rate. Of the 10 second nests that failed, one was abandoned, another succumbed to predation, and eight failed for unknown reasons.

Second nest attempts may be related to length of growing season. More days of favorable weather, coupled with the fact that breeding begins very early here, afford ample opportunity for rearing two broods most years. Food is generally available for a longer period as well. As shown in this study, up to one-third of all shrike pairs may attempt second nests during normal years (Table 2), but the vagaries of weather often prevent it.

In cases where nests were found empty but intact, predation was strongly suspected. Known nest predators common to the area included housecats (*Felis domesticus*), various snakes, and grackles (*Quiscalus mexicanus* and *Q. quiscula*).

In this study, the probability of survival from the start of incubation until fledging for 109 nests was 46%. Except for Alabama (Siegel 1980), where it was 43.2%, this figure is low compared to other studies. For instance, it was 62.2% in Colorado, 69.1% in Missouri, and 72% in Illinois (Graber et al. 1973, Porter et al. 1975, Kridelbaugh 1983).

Local nesting habitat appears to be still relatively abundant, so explanations for the shrike's gradually failing numbers must be sought elsewhere. In this intensely agricultural region, insecticides are widely used,

but the relationship between them and declining shrike populations is difficult to establish. The continuing loss of native grasslands to plowing eliminates valuable shrike foraging habitat. Luukkonen (1987) found that 11 nests surrounded by pastures produced twice the number of young shrikes as did nests in other habitats. Even if these fields are reseeded in later years, it is seldom done with native grasses.

Inadvertent destruction of some nesting habitat (i.e., Osage orange hedgerows) is also occurring. Because of their durability, Osage orange posts were formerly widely used to support barbed wire fences. Over the years, and in widespread localities, these posts grew into tree rows. The prevailing current tendency, however, is to replace them with metal or creosote-treated posts, completely eliminating this valuable tree so often used for shrike nesting (Table 1).

The future outlook for survival of the Loggerhead Shrike in this part of its range is not good. With a mean survival rate of only 46%, the steady decline in its numbers is bound to continue if populations do not stabilize.

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COMMUNAL ROOSTING OF COMMON RAVENS IN SOUTHWESTERN IDAHO

KATHLEEN A. ENGEL,[1] LEONARD S. YOUNG,[2] KAREN STEENHOF,[2] JERRY A. ROPPE,[1] AND MICHAEL N. KOCHERT[2]

ABSTRACT.—From 1983–1987, Common Ravens (*Corvus corax*) used thirteen communal roosts on a segment of electrical transmission line that runs 597 km from south-central Idaho to south-central Oregon. Up to 2103 ravens were counted at a single roost that spanned approximately six km of transmission line and 15 transmission towers. Most roosts were occupied between spring and autumn; one was occupied year-round. Peak numbers of ravens at most roosts and peak numbers of occupied roosts occurred during late summer and early autumn. Ravens concentrated on the highest portions of transmission towers, although more ravens roosted on the lower portions of towers when winds exceeded seven km/h. Ravens arrived at roosts earlier relative to sunset during summer than during spring or fall. Soon after fledging, juvenile and adult ravens left nesting areas and moved as far as 60 km to communal roosts. Some ravens used more than one communal roost during a year, moving between roosts up to 63 km apart. *Received 19 Feb. 1991, accepted 10 July 1991.*

Communal roosting is a prominent behavioral feature of the Corvidae (Goodwin 1976). Although roosting aggregations of up to several hundred Common Ravens (*Corvus corax*) have been observed throughout the northern hemisphere (Table 1), little is known about raven roosting behavior or roost site selection. Furthermore, there has been no published account of ravens roosting on power lines. In southwestern Idaho and southeastern Oregon, large concentrations of Common Ravens roosted on towers of Pacific Power's Malin to Midpoint 500-kV transmission line. This apparently unique situation provided an ideal opportunity to observe and document the roosting behavior of Common Ravens. Herein, we describe the temporal and spatial patterns of roost use and the behavior of ravens roosting on this transmission line.

STUDY AREA

The Malin to Midpoint 500-kV transmission line was constructed during 1980–1981 and runs 713 km (442 miles) from the Midpoint Substation, Jerome County, Idaho (line-mile 0) to the Malin Substation, Klamath County, Oregon (line-mile 442; Fig. 1). The line can be divided into two distinct segments separated by the Summer Lake Substation, Lake County, Oregon, located at line-mile 370. Fieldwork was limited to the area east of the Summer Lake Substation.

[1] Environmental Services Dept., Pacific Power, 920 S.W. Sixth Ave., 800 PFFC, Portland, Oregon 97204. (Present address KAE: Dept. of Wildlife Ecology, Univ. of Wisconsin, Madison, Wisconsin 53706.)
[2] Snake River Birds of Prey Research Project, Bureau of Land Management, 3948 Development Ave., Boise, Idaho 83705. (Present address LSY: Washington Dept. of Natural Resources, Forest Land Management Div., MQ-11, Olympia, Washington 98504.)

TABLE 1

CHARACTERISTICS OF COMMUNAL ROOSTS OF COMMON RAVENS

Location	Peak count	Substrate	Season of use	Reference
California, USA	200	brushy canyon	autumn–winter	Cushing 1941
England, UK	120	crags	winter	Fergusson 1943
Iraq	100+	trees	winter	Hutson 1945
Wales, UK	70	trees	year–round	Cadman 1947
Scotland, UK	32	crags	not reported	Coombes 1948
Scotland, UK	276	not reported	not reported	Campbell 1956
England, UK	86	trees	winter–spring	Hurrell 1956
Michigan, USA	61	not reported	summer	Mahringer 1970
Virginia, USA	106	trees	winter	Lucid and Conner 1974
Alaska, USA	10	abandoned buildings	winter	Temple 1974
Alaska, USA	800–900	not reported	autumn–winter	Brown 1974
Alaska, USA	160	trees	spring–summer	Brown 1974
Oregon, USA	836	marsh vegetation	autumn–winter	Stiehl 1981
Scotland, UK	300+	oil tanks/cliffs	not reported	Ewins et al. 1986
Scotland, UK	300+	cliffs	summer	Ewins et al. 1986
Germany	620[a]	trees	year-round[b]	Sellin 1987

[a] Peak counts ranged from 40–620 ravens.

[b] Twelve roosts were occupied for periods up to six months during different seasons.

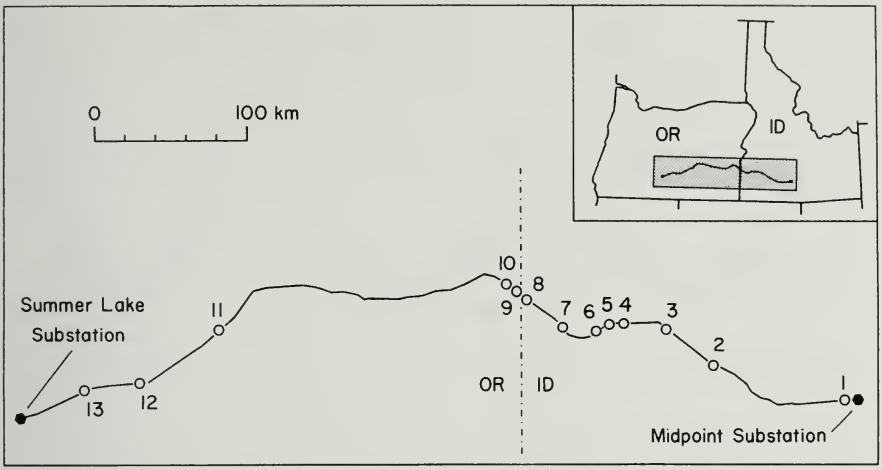

FIG. 1. Communal roosts of Common Ravens located on the Malin to Midpoint 500-kV transmission line, 1983–1987. Numbers refer to roosts described in Table 2.

Our study area encompassed a 125-km segment of line (line-miles 83–160) located in southwestern Idaho and extreme southeastern Oregon (Fig. 1). The free-standing steel-lattice towers (Fig. 2) are 25–47 m high and spaced approximately 300–400 m apart. In Idaho, the power line follows the relatively flat, deep-soiled Snake River plain. At the Oregon border, the Snake River heads north while the line continues west into more rolling topography. The area is dominated by livestock-grazed shrubsteppe vegetation (West 1983) and agriculture. From 1978–1987, mean annual temperature averaged 10.1 ± 1.1°C, and annual precipitation averaged 36.4 ± 7.8 cm (U.S. Dept. of Commerce, unpubl. data). Each year, about two-thirds of the annual precipitation fell from October to March.

METHODS

Roost surveys.—From April 1984 to November 1988, we surveyed the study area once each month to locate new communal roosts and to identify reoccupancy of previously used roosts on the transmission line. We considered a "roost" to be a collection of one or more adjacent transmission towers each with a concentration of at least three ravens perched together after sunset or before sunrise. Family groups of ravens roosting on towers at or near their nest sites during the fledging period (late May to mid-July) were not considered communal roosts.

From April 1984 to September 1985, we surveyed the study area primarily from the air. From then on, we surveyed the line from the ground. Surveys were flown as late in the evening as possible without compromising either our safety or ability to see roosting ravens. Aerial surveys began approximately 10 min after sunset on clear nights and five min after sunset on overcast nights. Ground surveys were performed by an observer who drove maintenance roads adjacent to the line and examined insulators for accumulated raven feces (i.e., contamination). In addition, we obtained information on roost occupancy over the entire transmission line opportunistically from routine maintenance patrols and nest surveys (Steenhof et al. 1987).

Throughout the study, we interviewed residents living near the transmission line to de-

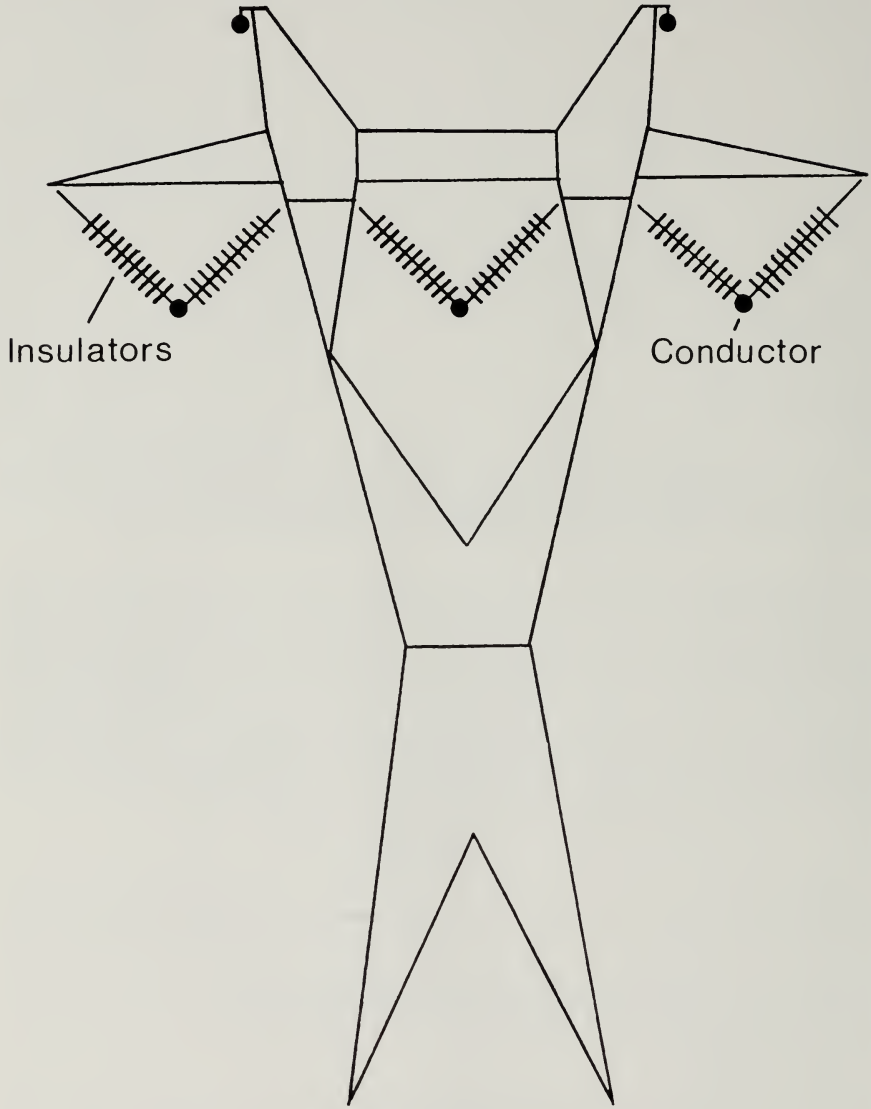

FIG. 2. Outline of a typical 500-kV transmission tower.

termine if ravens had been roosting in the vicinity of the transmission-line roosts before the line was constructed.

Roost observations.—In 1983, we observed one raven roost (Pleasant Valley Road) once a month to monitor temporal trends in the numbers of ravens there (Steenhof 1983). Then from 1984–1987, we observed selected raven roosts in the study area one to three evenings/

week to further describe raven roosting behavior, use of towers, and temporal trends in raven numbers (Young and Engel 1988).

Roost observations were made from a vehicle parked at a good vantage point usually at least 400 m from the nearest occupied roost tower. Observations began by 10 min before sunset and continued until it was too dark to count ravens accurately (usually 30 min after sunset). Every 10 min, an observer recorded the number of ravens perched on each of 10 tower sections of every occupied roost tower (Fig. 2). Each evening, the maximum number of ravens counted during a single 10-min interval was considered the total count for that roost. Percent cloud cover, wind velocity, and presence of precipitation were also recorded during each roost observation. Wind velocity was measured with a hand-held anemometer. In addition, during 1984–1986 and 1988, exact times of first arrival were recorded during roost observations. "Time of first arrival" was defined as the time after which at least one raven was present continuously on a roost tower.

Two all-night observations were made at the Initial Point Roost in June 1984 to determine whether ravens moved among towers during the night. A night scope (U.S. Army, AN-TVS4) was used to make these observations.

From April 1984 to November 1988, we simultaneously observed all occupied roosts on the transmission line east of the Summer Lake Substation once each month to monitor temporal trends in the number of ravens roosting on the line at one time. Other raven roosts (off the line) found in the study area were also observed during these "simultaneous" counts to obtain an estimate of the trends in the total number of ravens roosting communally in the study area. Procedures for these "simultaneous" counts were the same as those described above, with at least one observer stationed at each roost.

Observing marked ravens.—During May and June 1984, we wing-marked 71 nestling ravens from nests on 500-kV transmission towers and 59 from nests on natural substrates to determine when and how far juvenile ravens traveled from their nests to join communal roosts (Young and Engel 1988). Color and position of markers denoted whether nestlings were from 500-kV transmission tower or natural-substrate nests. Each marker bore a single digit; numbers in combination identified the specific nest from which individual ravens came.

During 1985–1987, we captured, transmitter-equipped, and radio-tracked 33 ravens as part of a study of their movements and habitat use (Young and Engel 1988). Twenty-four ravens (16 adults, seven subadults, one juvenile) were trapped at feeding areas near roosts, and nine were hand-captured as fledglings (ca 35–40 days old) at their nests. Transmitter-equipped ravens were tracked during four randomly selected days each week. One raven was tracked on each observation day from the time it left its roost in the morning until it returned to its roost in the evening. In addition, roost locations of transmitter-equipped ravens were determined one to four nights per week to document movements of ravens among roosts. Roost locations were determined by an observer with a hand-held antenna who checked each roost in the study area between one hour after sunset and one hour before sunrise.

Data analysis.—We used one-way analyses-of-variance (ANOVA) to test for differences in the percentage of ravens roosting on upper tower sections among roosts. Tower sections were grouped into "upper" and "lower" sections, located above and below the tower insulators, respectively (Fig. 2). If a significant difference was found, Tukey's Honestly Significant Difference (Tukey HSD) tests were used to determine between which roosts significant differences existed. Individual tower-nights were the sample units for tower-use analyses. Data collected from the Wilson Creek Roost after 1984 were excluded from tower-use analyses, because perch-deterrent devices were installed on towers at this roost in 1985 as part of another study (Young and Engel 1988). Only nights with no wind (<1 km/h) were

included in these analyses, because wind appeared to influence the vertical distribution of ravens among tower sections (Young and Engel 1988). Due to small sample sizes, inter-roost comparisons of tower use could be made only among the Initial Point, Marsing Dump, and Marsing Southwest roosts.

We used two-way ANOVA to examine the effects of wind velocity and the presence of precipitation on the percentage of ravens roosting on upper tower sections. Wind velocities were grouped into three categories for analysis: no wind, moderate winds (>0 km/h and <8 km/h), and high winds (≥8 km/h). If we found a significant wind effect and no significant interaction between wind and precipitation effects, we then used one-way ANOVA followed by Tukey HSD tests to locate between which wind velocities significant differences existed.

We used two-way ANOVA to test for month and cloud cover effects on times of first arrival. Percent cloud cover was grouped into three categories for analyses: clear skies (≤20% cloud cover), partly cloudy (>20% and <80% cloud cover), and overcast (≥80% cloud cover). If we found a significant month or cloud cover effect and no significant interaction between month and cloud cover effects, we then used one-way ANOVA followed by Tukey HSD tests to locate between which months or amounts of cloud cover significant differences existed. Individual roost-nights served as the sample units for these analyses.

All percentages were arcsine transformed (Zar 1974) before analysis. Statistical tests were evaluated at the 0.05 level of significance.

RESULTS

Use of roosts.—Large concentrations of roosting ravens were first observed on the transmission line in 1982, less than one year after the line was constructed. From 1983–1987, we located 13 communal raven roosts on the line, eight of which were within our study area (Fig. 1). Distances between adjacent transmission-line roosts in the study area averaged 12.4 km, ranging from 0.8 (Initial Point to Swan Falls Road) to 25.4 km (Wilson Creek to Marsing Dump). Five roosts (i.e., Initial Point, Swan Falls Road, Wilson Creek, Marsing Dump, and Marsing Southwest) were considered "major" roosts based on the relatively high numbers of ravens involved and the length of time each roost was occupied (Table 2). All major roosts we found were located on the transmission line in our study area during the first year surveys were made; no new major roosts developed on the line after 1984.

Interviews with local residents in the study area indicated that each of the major roosts was situated in an area where ravens roosted communally before the line was constructed; these earlier roosts occurred on rock outcrops, scattered clumps of low trees, and smaller transmission lines.

Ravens in the study area did not roost exclusively on the 500-kV transmission towers. Four communal roosts were found within 10 km of the transmission line by following transmitter-equipped ravens; three were on a 138-kV distribution line, and one was on the ground in mixed shrub-grass rangeland. Ravens also roosted occasionally on the ground adjacent to occupied transmission-line roosts.

The largest roosts on the transmission line were located within our

study area. Maximum numbers of ravens counted at seven of the eight transmission-line roosts in the study area exceeded 500, whereas no more than 150 ravens were counted at the other transmission-line roosts (Table 2). The highest count at a single roost (Initial Point) was 2103 on 22 July 1984. Relative sizes of the major transmission-line roosts were consistent from year to year. Each year, numbers of ravens were highest at the Initial Point Roost, followed by Marsing Southwest, Marsing Dump, and then the Wilson Creek or Swan Falls Road roosts.

From year to year, use of the transmission line by roosting ravens was highest in the late summer to early autumn and lowest during winter. Total numbers of ravens roosting on the line during simultaneous counts ranged from zero to 2121, with numbers being highest in July–September and lowest in January–March (Fig. 3). Peak numbers of ravens at most transmission-line roosts (10) occurred generally during late summer and early autumn, although peak numbers occurred during spring or autumn at Swan Falls Road and Wilson Creek and during autumn and winter at Marsing Southwest (Table 2). Peak numbers of both roosting ravens and occupied roosts tended to coincide. Between zero and six transmission-line roosts were occupied on a single night, with the highest number of roosts occupied during July–September and the lowest during November–February.

Annual roost occupancy from 1983–1987 ranged from one to five years; five roost sites (Midpoint, Hot Springs, Ditto Creek, Alkali Creek, and Moon Reservoir) were occupied briefly ($\leq$2 months) and during only one year (Table 2). Almost all transmission-line roosts (12) were occupied only between spring and autumn, but the Marsing Southwest Roost was occupied throughout the year. The length of time that individual roosts were occupied during a year ranged from one (e.g., Midpoint and Ditto Creek roosts) to 12 months (Marsing Southwest). The length of time each major roost was used was relatively consistent among years, although length of use of one major roost (Swan Falls Road) declined during the study.

Use of towers.—Within roosts, both numbers of towers used and numbers of ravens per tower varied considerably among nights. The number of towers used simultaneously at a roost ranged from one to 15 (Initial Point Roost), spanning up to six km of line. Numbers of ravens roosting on a single tower ranged from three to over 700. At each roost, ravens tended to concentrate on the centrally located towers within a span of occupied roost towers. However, ravens were never observed roosting on towers supporting nests occupied by ravens during the breeding season, even if the nest tower was located within a span of occupied roost towers.

Overall, 92% of the ravens observed roosting on transmission towers

TABLE 2

USE OF COMMUNAL ROOSTS BY COMMON RAVENS ON THE MALIN TO MIDPOINT 500-KV TRANSMISSION LINE, 1983–1987

Roost (line-miles)	Periods of occupancy		No. of ravens		
	Year	Months[b]	$\bar{x}$ (SD)	Max. (month)	N
1.[a] Midpoint (2)	1986	Oct.	—[c]	—[c]	—[c]
2. Hot Springs (61)	1985	May–June	22 (0)	22 (June)	1
3. Ditto Creek (85–86)	1986	Sept.	42 (0)	42 (Sept.)	1
4. Pleasant Valley (101–103)	1983	Feb.–Sept.	181 (247)	620 (July)	5
	1984	July–Aug.	77 (95)	144 (Aug.)	2
5. Initial Point (106–113)	1984	Apr.–Sept.	835 (398)	2103 (July)	63
	1985	Mar.–July	460 (269)	1075 (July)	58
	1986	Apr.–Nov.	532 (441)	1226 (Aug.)	8
	1987	May–Dec.	571 (390)	1339 (Aug.)	36
6. Swan Falls (114–117)	1984	Apr.–Oct.	110 (133)	359 (Oct.)	165
	1985	Aug.–Sept.	379 (126)	543 (Aug.)	11
	1986	Mar.–May, July–Sept.	175 (202)	540 (Mar.)	6
	1987	Mar., June, Aug.	13 (8)	27 (Mar.)	9
7. Wilson Creek (131–132)	1984	Apr.–Oct.	245 (135)	559 (Oct.)	11
	1985	Mar.–Aug.	123 (85)	298 (May)	42
	1986	Mar.–Oct.	66 (40)	137 (Apr.)	31
	1987	Mar.–May, July–Dec.	115 (118)	334 (Sept.)	26
8. Marsing Dump (148–150)	1984	Aug.–Sept.	427 (264)	613 (Aug.)	2
	1985	Jan.–May, July–Oct.	284 (253)	945 (Oct.)	49
	1986	Jan., Mar.–Dec.	299 (198)	621 (Nov.)	11
	1987	Jan.–Dec.	233 (164)	543 (Oct.)	43
9. Marsing Southwest (153–156)	1984	Apr.–Dec.	311 (188)	690 (Dec.)	17
	1985	Jan.–May, July–Oct.	284 (253)	945 (Oct.)	49
	1986	Jan., Mar.–Dec.	299 (198)	621 (Nov.)	11
	1987	Jan.–Dec.	233 (164)	543 (Oct.)	43

TABLE 2
CONTINUED

Roost (line-miles)	Periods of occupancy		No. of ravens		
	Year	Months[b]	$\bar{x}$ (SD)	Max. (month)	N
10. Alkali Creek (160)	1985	Nov.	701 (0)	701 (Nov.)	1
11. Moon Reservoir (283–284)	1986	Aug.	136 (0)	136 (Aug.)	1
12. Wagontire (321–322)	1984	June–Oct.	101 (58)	148 (July)	4
	1985	July	37 (0)	37 (June)	1
13. Christmas Valley (342)	1984	July	63 (0)	63 (July)	1
	1985	July	12 (0)	12 (July)	1

[a] Numbers refer to locations on Figure 1.
[b] Systematic surveys did not begin until April 1984 and covered only line-miles 83–160.
[c] Occupancy of this roost was identified through ground surveys.

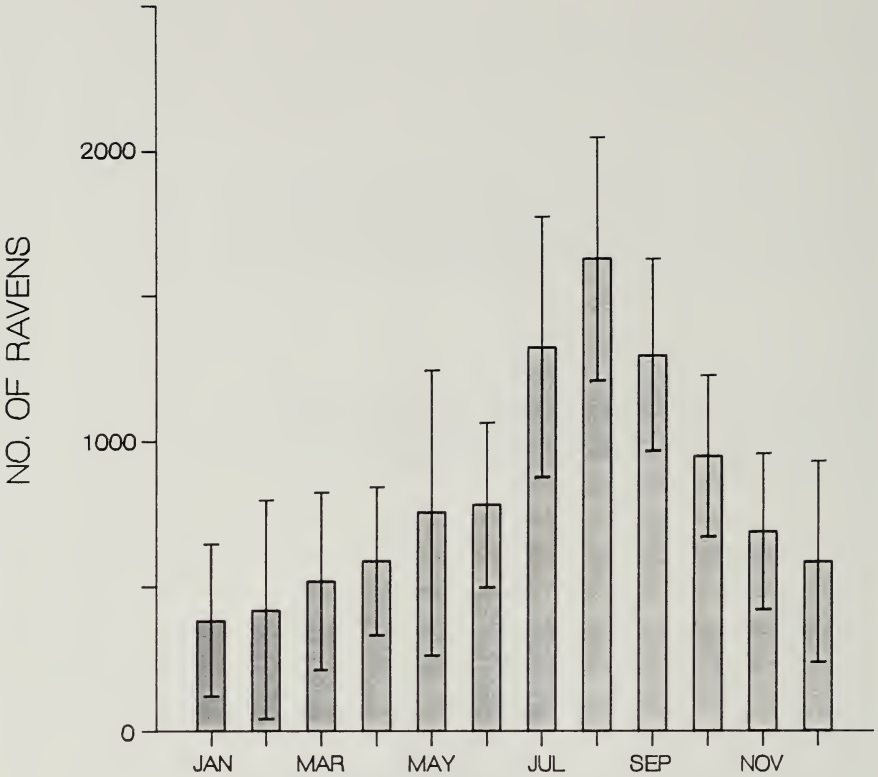

FIG. 3. Mean numbers of Common Ravens counted on the transmission line during monthly simultaneous observations, April 1984–November 1988.

roosted on upper tower sections above insulators. The percentage of ravens roosting on upper tower sections did not differ significantly between nights with and without precipitation (two-way ANOVA, $F = 1.87$, df = 1, 1403, $P = 0.17$); however, the percentage of ravens on upper tower sections did differ significantly among nights with different wind velocities (two-way ANOVA, $F = 47.11$, df = 2, 1403, $P < 0.01$). A significantly higher percentage of ravens roosted on upper tower sections during nights with no to moderate wind (95% and 92%, respectively) than during nights with stronger winds (77%; one-way ANOVA, $F = 54.66$, df = 2, 1406, $P < 0.01$; Tukey HSD Ps < 0.01).

Although the percentage of ravens roosting above insulators on windless nights differed significantly among roosts (one-way ANOVA, $F = 6.43$, df = 2, 608, $P < 0.01$), the majority (>93%) of ravens at each roost used upper tower sections. During evenings with no wind, the percentage of

ravens roosting above insulators was significantly higher at the Marsing Southwest Roost (97%) than at the Initial Point Roost (94%; Tukey HSD $P < 0.05$).

Roosting behavior.—Ravens gathered at staging areas before roosting, converging from a variety of foraging areas. Staging areas were almost always open and sparsely vegetated. Some staging areas were located at the bases of roost towers; others were several km away. Ravens usually flew from staging areas to roost towers singly, in pairs, or in small groups (<10 individuals). However, the entire staging aggregation sometimes flew to the roost simultaneously.

Ravens began to roost on towers between one hour before and 35 min after sunset and usually continued to land on towers until dark. Maximum counts were almost always obtained during the last count interval. Mean time of first arrival on towers was 13 ± 22 min before sunset (N = 347 roost-nights). Times of arrival did not differ significantly among clear, partly cloudy, and overcast evenings (two-way ANOVA, $F = 2.50$, df = 2, 302, $P = 0.08$); however, arrival times did differ significantly among months (April–October; two-way ANOVA, $F = 5.01$, df = 6, 302, $P < 0.01$; Fig. 4). Times of first arrival tended to be earlier with respect to sunset during the summer months than during other times of year; arrival times were significantly earlier relative to sunset during June and July than during all other months (one-way ANOVA, $F = 10.01$, df = 6, 316, $P < 0.01$; Tukey HSD Ps < 0.05).

Ravens exchanged positions repeatedly on roost towers before settling down approximately one hour after sunset. No nocturnal movement was observed during two all-night observations. Ravens usually began to leave roost towers before dawn. Transmitter-equipped ravens were observed leaving roosts in total darkness as early as 45 min before sunrise. Ravens often gathered at staging areas immediately, but sometimes they flew directly to foraging areas. Occasionally, large numbers of ravens were also observed on roost towers during the day.

Roosting ravens occasionally shared towers with raptors, including Red-tailed Hawks (*Buteo jamaicensis*), Ferruginous Hawks (*B. regalis*), and Prairie Falcons (*Falco mexicanus*). Raptors almost always roosted on lower tower sections below ravens. Ravens usually ignored Golden Eagles (*Aquila chrysaetos*) perched beneath them on lower tower sections; however, when an eagle perched on an upper tower section of an occupied roost tower, ravens often harassed the eagle, rising repeatedly from the tower as a group to mob it. Ravens usually settled down by dark, and they were never observed roosting within 4–5 m of an eagle on an upper tower section.

Ravens in the study area did not always roost communally. Transmitter-

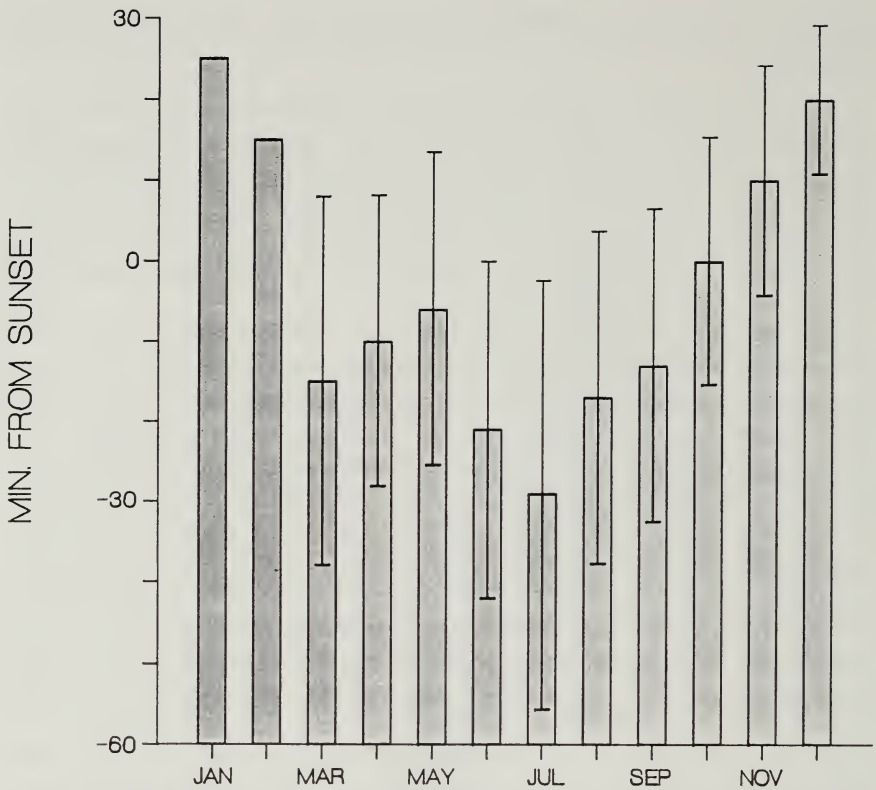

FIG. 4. Mean monthly times of arrival of Common Ravens to communal roosts, April 1984–December 1986 and January–November 1988.

equipped breeding ravens usually roosted at their nest sites during the breeding season and occasionally roosted at their nest sites during other times of year. In addition, one subadult transmitter-equipped raven was observed roosting alone on the ground in a cornfield approximately one km from the nearest communal roost.

Movements of ravens among roosts.—Numbers of roost locations obtained for 32 transmitter-equipped ravens ranged from two to 163 (insufficient data were collected for one transmitter-equipped raven). Twenty transmitter-equipped ravens used more than one roost during the periods they were tracked. Individual ravens were observed using from one to six different roosts. The maximum number of movements observed between roosts was exhibited by one raven that changed roosts 19 times over a period of 209 days. Conversely, the longest period an individual raven was observed using a single roost was 209 days at the Marsing Southwest

Roost. In general, the number of times a transmitter-equipped raven moved to other roosts increased with the length of time it was tracked; of the 11 ravens that were not observed changing roosts, nine were tracked for a relatively short period of time ($\leq$3 months), and four were tracked during winter when only one roost (Marsing Southwest) was occupied. However, among those birds for which roost locations were obtained at least once per week, one raven used two roosts in a period of two days, and another used only one roost over 120 days.

Movements of ravens occurred between all transmission-line roosts in the study area, including those up to 63 km apart (Initial Point to Marsing Southwest). Frequency of movements between roosts was not related entirely to the distance between roosts. Movements of ravens among transmission-line roosts were most frequent between the Initial Point and Marsing Southwest roosts (nine movements), followed by movements between the Initial Point and Swan Falls Road roosts (six movements).

Incorporation of juvenile ravens.—We made 85 sightings of wing-marked (but not transmitter-equipped) juvenile ravens within 400 m of a communal roost. Forty-five (53%) sightings were of ravens from transmission-tower nests, and 22 (26%) were of ravens from natural-substrate nests (18 sightings were not identified). During 1984, the year these ravens were marked, we began seeing wing-marked fledglings at the Initial Point Roost in early July; three of these sightings were of fledglings from a natural-substrate nest approximately 24 km away from the roost.

We obtained more detailed information on incorporation of fledgling ravens into communal roosts from the five transmitter-equipped fledgling ravens. Dates of incorporation occurred from eight to 41 days after transmitter attachment ($\bar{x} = 23 \pm 12$ days), when the ravens were between 43 and 81 days old. Four of the juvenile ravens first joined roosts on the 500-kV transmission line; however, one juvenile first joined a roost on a nearby 138-kV distribution line. Notably, this raven was the only transmitter-equipped juvenile from a natural-substrate nest. Juvenile ravens did not always first join the roost closest to their nests. One juvenile initially joined a roost 50 km from its nest, and another raven joined one 60 km away. In contrast, juvenile ravens from two nests within the Initial Point Roost first joined that roost.

DISCUSSION

Three main aspects of the roosting behavior of ravens we observed were similar to those exhibited by many other communally roosting species. First, most communally roosting birds studied use the same roost sites year after year (Eiserer 1984). Although five roost sites on the transmission line were occupied for less than two months and during only one

year, most roost sites on the line were used during successive years. Intermingling of birds among local communal roosts such as we observed is also common (Caccamise et al. 1983).

Second, seasonal fluctuations in numbers of birds at a communal roost are typical (Eiserer 1984). Similar to ravens in our study, roosting flocks of European Starlings (*Sturnus vulgaris*) and Common Grackles (*Quiscalus quiscula*) increased through early summer, peaking in mid-August and then declining through fall (Caccamise et al. 1983). The seasonal changes in numbers of ravens at the communal roosts we observed likely reflect changes in both the proportion of the local population using communal roosts and in the size of the local raven population. The summer increase in ravens at communal roosts was probably due to an influx of nesting birds and their newly fledged young; peak numbers of roosting ravens coincided with the post-fledging period, and all marked juvenile ravens joined communal roosts during this time. On the other hand, autumnal declines in overall numbers of ravens using communal roosts may have been due to dispersal of some birds out of the study area, with those remaining shifting to the Marsing Southwest Roost for the winter. All (six) transmitter-equipped ravens that remained in the study area until winter moved to the Marsing Southwest Roost when this roost was increasing in size and other roosts were being evacuated.

Third, roost approaches typically tend to occur at higher light intensities than do roost departures (Eiserer 1984). Ravens may leave roosts at lower light intensities than they enter them simply to take advantage of early morning foraging opportunities (Counsilman 1974) or because of an immediate need for food upon waking (Seibert 1951). Although cloud cover does not appear to influence roosting time in some birds (Young 1971), the lack of relationship we found between cloud cover and roosting time may have been due to our method of measurement. Illumination level may influence the timing of initial movements of ravens toward their roosts more than it influences the timing of arrival at the roost, as observed in starlings (Davis and Lussenhop 1970). Seasonal differences in the timing of roosting flights have also been observed in other species where, similar to ravens in this study, roosting times were earliest during summer (Davis 1955, Meanley 1965, Gyllin and Kallander 1976); however, the reasons for these differences remain unclear (Eiserer 1984).

There are, however, three unique aspects of the raven roosts on the Malin to Midpoint transmission line. First, these are the largest known roosts of Common Ravens in the world (Table 1). Before this study, the largest reported roosts included one of up to 800–900 ravens near Fairbanks, Alaska (Brown 1974) and another in the Harney Basin, Oregon, where a peak of 836 ravens was recorded (Stiehl 1981). The peak count

of 2103 ravens recorded at the Initial Point Roost is more than twice the number of ravens observed at either of the other roosts.

The relatively large sizes of the raven roosts we observed were likely due to locally abundant food sources and nest sites for ravens. In our study area, foods associated with agriculture comprise a large part of the diet of ravens year-round and are abundant throughout the year (Engel and Young 1989). Furthermore, cliffs of the Snake River Canyon, numerous buttes and rock outcrops, and the transmission towers together provide abundant nest sites for ravens in our study area. As many as 128 raven pairs nest in the Snake River Canyon (USDI 1979), and in 1987, 35 pairs of ravens nested on the 500-kV transmission-line towers in our study area (Steenhof et al. 1987).

The second unique aspect of the transmission-line roosts is that they involve man-made structures, whereas most raven roosts reported in the literature occurred on natural substrates (Table 1). Ewins et al.'s (1986) report of ravens roosting on oil storage tanks, and Temple's (1974) observations of ravens roosting in abandoned buildings, are the only previously published records of Common Ravens roosting on man-made structures. Although ravens did not roost exclusively on transmission towers during our study, towers appeared to present an attractive alternative to other roost sites. Ravens roosting on transmission towers may be less susceptible to predation than those roosting closer to the ground or in trees and rock outcrops. In addition, the transmission towers may provide safe roosting sites that are also in closer proximity to local food sources than alternative sites.

Lastly, the roosts we observed were used predominately during spring to autumn, and one was occupied year-round. Most raven roosts reported in the literature were occupied in autumn and winter, excluding a spring/summer roost of up to 160 ravens in Alaska (Brown 1974) and a summer roost of up to 61 ravens in Michigan (Mahringer 1970; Table 1). Furthermore, only two previously reported raven roosts (Cadman 1947, Sellin 1987) were occupied year-round. The perennial food supply provided by agricultural activities in our area may have facilitated the year-round occupation of the Marsing Southwest Roost.

ACKNOWLEDGMENTS

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BREEDING DISTRIBUTION OF THE BLACK TURNSTONE

Colleen M. Handel and Robert E. Gill, Jr.[1]

Abstract.—Eighty-five percent of the world population of Black Turnstones (*Arenaria melanocephala*) nest on the central Yukon-Kuskokwim Delta, Alaska, 65% concentrated in a narrow band of salt grass, graminoid, and dwarf shrub meadows within two km of the coast. An estimated 61,000 to 99,000 birds (95% CI), with a point estimate of 80,000 birds, breed on the central delta. About 15,000 others nest elsewhere in Alaska. Abundance varies among habitats and with distance from the coast. On the central delta, highest breeding densities occur in coastal salt grass meadows (1.11 ± 0.16 birds·ha^{-1}) and lowest densities occur on dwarf shrub mat tundra (0.04 ± 0.04 birds·ha^{-1}). Breeding densities in mixed graminoid and dwarf shrub meadows decline significantly with distance from the coast, decreasing abruptly from 0.75 ± 0.11 birds·ha^{-1} within the first two km to 0.09 ± 0.03 birds·ha^{-1} farther inland. Although salt grass meadows constitute only 5% of the coastal lowlands, they support 25% of the population. *Received 5 April 1991, accepted 6 Aug. 1991.*

The Black Turnstone (*Arenaria melanocephala*) is one of the most maritime of New World shorebirds. The entire world breeding population is restricted to coastal habitats of western Alaska, where the birds breed from early May to late July (Handel 1982) before moving to wintering areas along the Pacific Coast from southcentral Alaska to central Mexico (AOU 1983). Little has been reported about the details of distribution or abundance of Black Turnstones within their breeding range. During a study of turnstone breeding ecology (Handel 1982), we conducted aerial and ground surveys of the Yukon-Kuskokwim Delta, an area for which published breeding records were most numerous (Conover 1926, Brandt 1943, Walkinshaw 1950, Gabrielson and Lincoln 1959, Kessel et al. 1964, Harris 1966, Holmes and Black 1973). Here we present results of these surveys, summarize previously unpublished breeding records, and identify habitats most important for breeding.

STUDY AREA

The Yukon and Kuskokwim rivers in western Alaska form the largest delta complex in North America, encompassing 129,500 km^2 (Thorsteinson et al. 1989). The delta predominantly is a flat plain of wet and moist tundra dotted with innumerable thaw lakes and crossed by meandering rivers, many of them active tributaries or former channels of the Yukon River (Wahrhaftig 1965; Dupré 1978, 1988). Shorebird habitats generally occur in bands parallel to the coast, changing along a gradient of increasing elevation and decreasing moisture and salinity. The coastal lowlands (Fig. 1) progress inland through a mixture of graminoid and dwarf shrub meadows up to 30 km inland. Storm surges regularly inundate

[1] Alaska Fish and Wildlife Research Center, 1011 East Tudor Road, Anchorage, Alaska 99503.

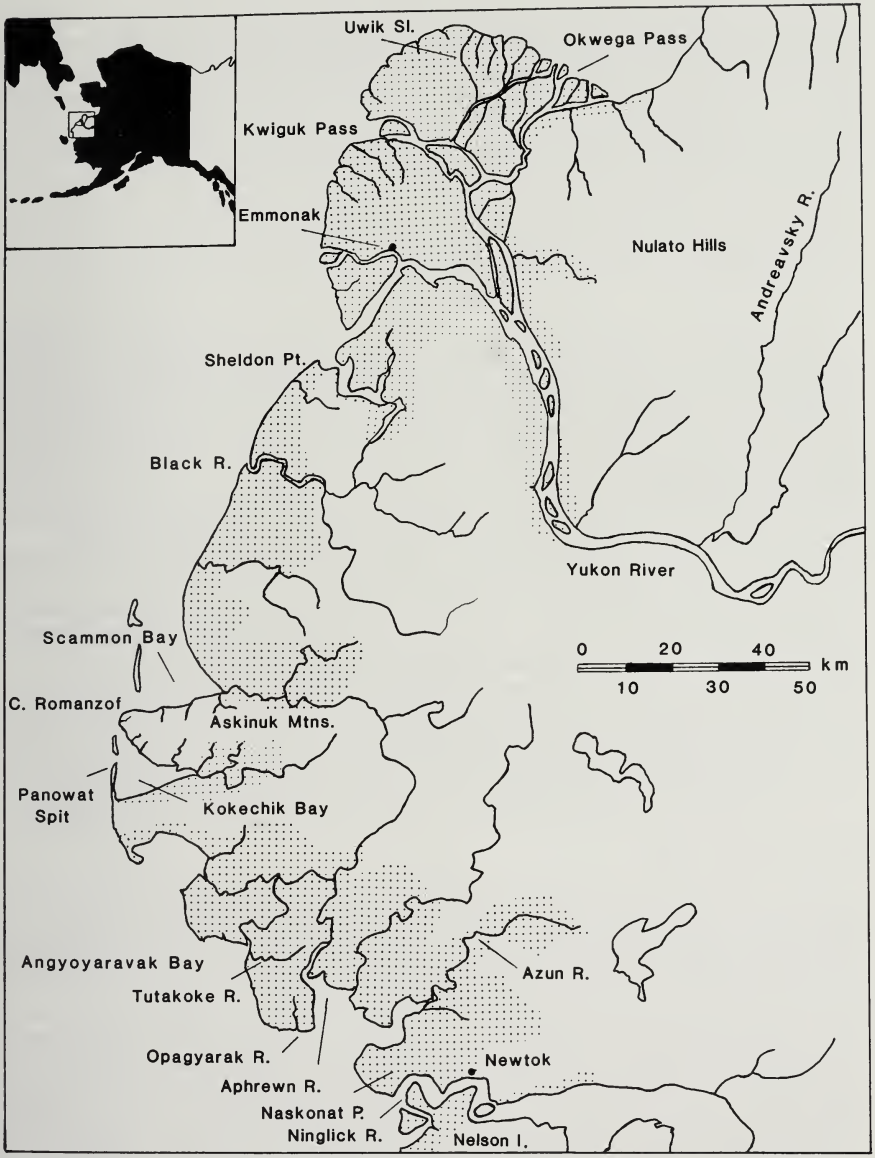

FIG. 1. The north and central Yukon-Kuskokwim Delta, Alaska, showing approximate extent of coastal lowlands (stippled area).

the coastal lowlands in late summer and fall (King and Dau 1981, Wise et al. 1981, Wise and Leslie 1988). Beyond are the uplands which are vegetated with dwarf shrub mat tundra not directly influenced by deltaic processes. On the active north delta, dwarf willows (*Salix* spp.) border coastal sloughs and tall thickets of willows and alders (*Alnus crispa*) occur farther inland (Jones and Kirchhoff 1977, Truett et al. 1984, Thorsteinson et al. 1989). Along the degrading, more tidally influenced central and southern portions of the delta, salt grass meadows dominated by *Carex ramenskii, Potentilla egedii,* and *Elymus arenarius* form "fingers" of habitat on eroding barren mudflats along the coast and at the mouths of major rivers. The central and southern parts of the delta are comparatively free of alder and willow thickets (Holmes and Black 1973, Jackson 1981, Tande and Jennings 1986).

METHODS

Museum searches.—We solicited data on egg sets and downy young of Black Turnstones from those museums listed by Kiff (1979) as having large oological holdings (see Acknowledgments). We used published and unpublished records to delineate the breeding range and to estimate relative abundance away from the Yukon-Kuskokwim Delta. A detailed summary of all breeding records is on file with the authors and with the University of Alaska Museum in Fairbanks.

Survey methods.—On 25 and 26 May 1978, we flew an aerial survey along 556 km of the Yukon-Kuskokwim Delta coastline from Okwega Pass south to Newtok, excluding a 97-km segment between Panowat Spit and the Tutakoke River (Fig. 1). We flew in a Cessna 185 on floats at an altitude of 60 m and a speed of 185 $km \cdot h^{-1}$. Two observers recorded all Black Turnstones within 100 m of each side of the aircraft as it flew parallel to and 200 m inland of the shoreline. One observer surveyed a second 100-m-wide aerial transect about 1 km inland of the shoreline from the Tutakoke River south to Newtok.

Between 30 May and 12 June 1981, we censused 25 randomly spaced ground transects perpendicular to the coast of Angyoyaravak Bay (Fig. 1). Transects were 30 m wide, averaged 3.1 ± 0.5 km in length (range 1.2–11.2 km), and were subdivided into 80-m long blocks. While walking parallel along the edges of each strip transect, two observers counted all turnstones flushing from or flying across each block. The predominant habitat within each block was classified as salt grass meadow, mixed graminoid and dwarf shrub meadow, or dwarf shrub mat tundra.

From 1978 to 1982, we monitored all nesting attempts on a 20-ha study plot in a mixed graminoid and dwarf shrub meadow along the coast of Angyoyaravak Bay (Handel 1982). Turnstones nesting on the study plot were captured and marked with unique combinations of colored leg bands. All nests on a second 20-ha plot in an adjacent salt grass meadow were monitored from 1978 to 1981 but no birds were color marked.

We used an electronic digitizing planimeter to measure the area of coastal lowland marshes and meadows between the Askinuk Mountains and the north side of Nelson Island (Fig. 1) as classified on 1:250,000 scale Landsat vegetation maps (Talbot et al. 1985). Since salt grass meadows were not discernible from this Landsat interpretation, their extent within 5 km of the coast was measured from color infrared aerial photographs (1:120,000 and 1:60,000) taken from 1970 to 1980 (U.S. Geological Survey, unpublished imagery).

Statistical analyses.—The distribution of turnstones within Angyoyaravak Bay was analyzed with respect to habitat type and distance from the coast. All 80-m blocks of the same predominant habitat within each transect were combined into single samples for comparison of densities. We used nonparametric procedures to test for differences among habitats and to measure linear relationships between densities and distance from the coast (Conover 1980). Statistical analyses were conducted using the SPSS (1990) software package, and differences were considered significant at the 0.05 level. Data are presented as mean ± standard error unless stated otherwise.

We stratified coastal lowlands before we estimated the size of the turnstone population nesting on the central Yukon-Kuskokwim Delta. Stratification was based on statistically significant differences among densities detected on ground transects in Angyoyaravak Bay in different habitats and at different distances from the coast. For each of the two study plots we then calculated the ratio between the known nesting density and the density detected on adjacent transects. We averaged these two ratios to obtain a correction factor ($\bar{c}$). The point estimate of the population total was obtained by the following formula: $T = \sum_{i=1}^{k} (\bar{d}_i \cdot \bar{c} \cdot a_i)$, where T = population total, k = number of strata, $\bar{d}_i$ = mean observed density in stratum i, $\bar{c}$ = mean correction factor for the two study plots, and a_i = area of stratum i.

To obtain confidence intervals for the population estimate, we calculated a bootstrap estimate for the standard error of the mean corrected-density for each stratum. First we randomly resampled (with replacement) the N original observed densities within each stratum for a bootstrap sample of size N. We then multiplied these by one of the two correction ratios (randomly selected) to obtain a bootstrap sample of N corrected-densities. This procedure was replicated for each stratum 100 times to estimate the distribution function and calculate the standard error of the mean corrected-density within each stratum. Using these standard errors, we calculated 95% confidence intervals for the population estimate within each stratum. Finally, we calculated the estimated variance and 95% confidence limits for the stratified population total: $95\%\ CI = T \pm 1.96 \cdot (\sum_{i=1}^{k} a_i^2[s_i^2])^{0.5}$, where T = population total, k = number of strata, a_i = area of stratum i, and s_i = standard error of the mean corrected-density in stratum i.

This population estimate was based on three assumptions: (1) that the densities detected on ground transects in Angyoyaravak Bay were a representative sample of those in other bays on the central delta; (2) that the densities detected on ground transects within 12 km of the coast were representative samples of those occurring up to 25 km inland within the same strata; and (3) that the correction factors calculated for the two study plots represented a random sample of such correction factors for other breeding areas sampled.

RESULTS

General breeding distribution and habitat.—We found 254 records of nests, egg sets, or downy young of Black Turnstones from 33 different locations in Alaska, including 15 previously unpublished sites (Table 1, Fig. 2). Most (60%) of the records, including three new nesting records from north Nelson Island, were from five coastal breeding areas on the central Yukon-Kuskokwim Delta in salt grass meadows and mixed graminoid and dwarf shrub meadows. South of the central delta, breeding records were found for seven new sites with similar habitats, including south Nelson Island, Kegaktuk Island just off Nunivak Island, and various sites along the Kuskokwim River as far inland as Bethel.

To the north, breeding was recorded for four new sites on the north Yukon Delta, two new sites on the Seward Peninsula, and one new site on the North Slope. Four of five nests found on the Yukon River for which habitat was recorded were situated on a small island and surrounded by willow stems; the fifth was on a narrow ridge of mossy tundra next to

TABLE 1
PREVIOUSLY UNPUBLISHED BREEDING LOCATIONS OF THE BLACK TURNSTONE

Region and site	Year	Record type	Collector or observer
North Slope			
Utukok River	1978–1982[a]	1 nest	J. Hechtel, pers. comm.
Seward Peninsula			
Kalik River	1991	1+ downy young	M. Stishov, pers. comm.
Arctic Lagoon	1991	1+ downy young	M. Stishov, pers. comm.
North Yukon Delta			
St. Michael	Unknown	1 egg set	C. L. Hall
"Mouth of Yukon"	1898	2 egg sets	J. H. Spencer
Kwikpak Pass, Yukon Rv.	1929	1 egg set	S. Warburton
Kwiguk, Yukon Rv.	1929	4 egg sets	S. Warburton
Central Yukon-Kuskokwim Delta			
N. Nelson Island	1910	1 egg set	J. Koren
N. Nelson Island	1967	2 nests	J. Hout, unpubl.
South Yukon-Kuskokwim Delta			
S. Nelson Island	1984	4 nests	R. Stehn, pers. comm.
Nunivak Island	1983	1 downy young	G. V. Byrd, W. Butler, pers. comm.
Kipnuk	1954–1955	3 egg sets	W. M. Batterson
"Near Quigillingok"	1930	3 egg sets	D. B. Bull
Kuskokwim Delta	1931	4 egg sets	D. B. Bull
Quinhagak	1934	3 egg sets	A. Johnson, "Native"
Bethel	1929–1930	2 egg sets	D. B. Bull

[a] Turnstones observed all five years; exact date of nest unknown.

a wet meadow (S. Warburton, unpubl. egg specimen records). On the Seward Peninsula, M. Stishov (pers. comm.) recorded 57 adults and several unfledged young on 3–4 July 1991 in salt grass and graminoid meadows along the inner beach of the Arctic Lagoon barrier spit. On 5–6 July 1991 he also recorded 52 adult Black Turnstones and several unfledged young in similar meadows along the Kalik River up to 2–3 km from the mouth. The most northern breeding record was that of a nest on the Utukok River in the Brooks Range. The nest was under a willow shrub on a gravel bar about 7 km below the confluence with Driftwood Creek (J. Hechtel, pers. comm.). Hechtel considered the species "common" along several kilometers of the river each summer he worked there (1978–1982). Identity was confirmed by D. D. Gibson (pers. comm.) from photographs of adults in the area.

FIG. 2. Locations of previously published (solid circles) and unpublished (open circles) breeding records of Black Turnstones. Questionable published breeding records are indicated by solid triangles.

Distribution along the Yukon-Kuskokwim Delta coast.—On aerial surveys in spring 1978, no turnstones were encountered along 135 km of coastline of the north Yukon Delta between Okwega Pass and Sheldon Point (Table 2). A single turnstone was sighted, however, on mudflats of an exposed bar in Kwiguk Pass, 17 km inland, when the plane landed for refueling at Emmonak (Fig. 1). Low numbers were encountered south along the coast between Sheldon Point and Scammon Bay (0.01 birds·ha^{-1}). Most of these were just south of the Black River. No turnstones were seen along the predominantly rocky coast around Cape Romanzof or along the sandy Panowat Spit (Fig. 1). Highest densities (0.17 birds·ha^{-1}) were detected along the coast of the central delta between Kokechik Bay and the Ninglick River (Table 2). The largest concentrations there occurred between the Opagyarak and Aphrewn rivers (0.32 birds·ha^{-1}) and on the Naskonat Peninsula (0.26 birds·ha^{-1}), although the coast between Panowat Spit and the Tutakoke River, including Angyoyaravak

TABLE 2

NUMBERS AND RELATIVE DENSITIES OF BLACK TURNSTONES OBSERVED DURING AERIAL SURVEYS ALONG COASTAL TUNDRA AND 1 KM INLAND ON THE YUKON-KUSKOKWIM DELTA, ALASKA, ON 25–26 MAY 1978

Area surveyed	Length of coast (km)	No. birds	No. birds·ha^{-1}
Along coast[a]			
North delta	135	0	0
Black River area	109	30	0.01
Central delta	150	499	0.17
One km inland[b]			
Central delta	128	67	0.05

[a] Strip transects along coast were 200 m wide. North delta = Okwega Pass–Sheldon Point; Black River area = Sheldon Point–Scammon Bay; central delta = Kokechik Bay–Newtok, excluding 55 km around Cape Romanzof and 10 km along Panowat Spit, where there were no turnstones, and 97 km between Panowat Spit and the Tutakoke River, which was not surveyed (Fig. 1).

[b] Strip transects 1 km inland were 100 m wide. Survey area = Tutakoke River–Newtok (Fig. 1).

Bay, was not surveyed. Densities 1 km inland were only about a third of those along the immediate coast (Table 2).

Distribution in relation to habitat and distance from coast.—The abundance of turnstones on ground transects surrounding Angyoyaravak Bay varied with habitat and with distance from the coast (Fig. 3). Highest densities were found in salt grass meadows with a significant peak at 3–4 km inland ($P = 0.045$, Kruskal-Wallis test), although sample sizes of salt grass habitat beyond 2 km from the coast were limited. Among 10 transects that included some salt grass meadows, overall detections averaged 2.83 ± 0.40 birds·ha^{-1}.

Intermediate densities occurred in mixed graminoid and dwarf shrub meadows (Fig. 3). In this habitat, bird abundance declined abruptly between 0 and 3 km from the coast ($P = 0.014$, $r_s = -0.41$) and more gradually farther inland ($P = 0.013$, $r_s = -0.32$). Turnstones were scarce (0.10 ± 0.10 birds·ha^{-1}, $N = 7$) on dwarf shrub mat tundra, which occurred predominantly inland. Combining all habitats except salt grass meadows, detection rates averaged 1.91 ± 0.30 birds·ha^{-1} ($N = 12$) within 2 km of the coast and fell to 0.23 ± 0.06 birds·ha^{-1} ($N = 13$) farther inland.

Estimate of true nesting densities.—Between 1978 and 1982, nesting densities averaged 0.95 ± 0.10 pairs·ha^{-1} in mixed graminoid and dwarf shrub meadow and 1.18 ± 0.15 pairs·ha^{-1} in salt grass meadow on the two study plots at the mouth of the Tutakoke River (Table 3). Densities were higher on salt grass meadow in every year except 1979.

During 1981, 4.34 ± 0.81 birds·ha^{-1} were detected on four transects near the first study plot, and 5.73 ± 0.52 birds·ha^{-1} were detected on

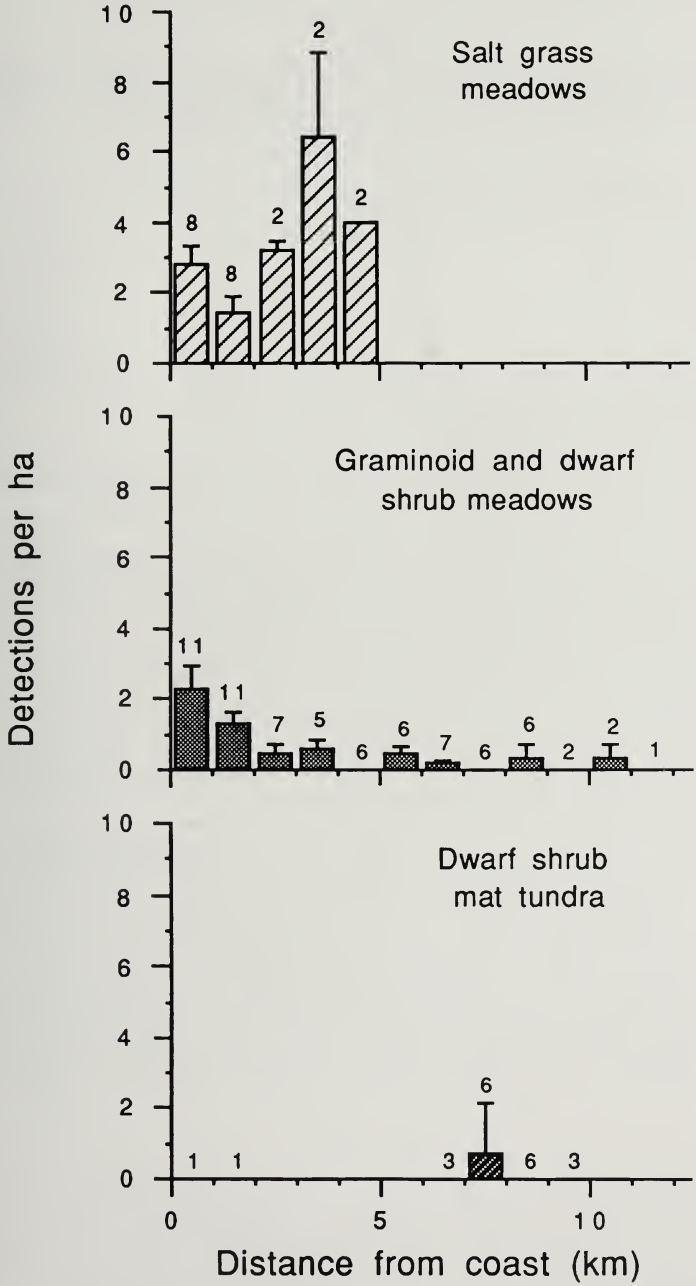

FIG. 3. Number of Black Turnstones detected per hectare during ground surveys in Angyoyaravak Bay, shown by habitat and distance from the coast. Data are shown as $\bar{x} \pm$ SE. The number of transects is indicated above each bar.

TABLE 3

NUMBER OF NESTS (EXCLUDING KNOWN OR SUSPECTED RENESTS) AND DENSITIES OF NESTING PAIRS OF BLACK TURNSTONES ON TWO 20-HA STUDY PLOTS IN DIFFERENT HABITATS AT THE MOUTH OF THE TUTAKOKE RIVER, ALASKA

	Graminoid and dwarf shrub meadow		Salt grass meadow	
Year	No. nests	Pairs·ha^{-1}	No. nests	Pairs·ha^{-1}
1978	18	0.90	29	1.45
1979	26	1.30	15	0.75
1980	21	1.05	25	1.25
1981	15	0.75	25	1.25
1982	15	0.75	—[a]	—[a]
$\bar{x} \pm$ SE	19 ± 2	0.95 ± 0.10	24 ± 3	1.18 ± 0.15

[a] Plot in salt grass meadow was not censused in 1982.

two transects near the second plot. The ratio between known nesting densities on the plots and those detected on nearby transects was 0.346 and 0.436 for the two plots, respectively. The mean correction factor was 0.391 nesting birds per detection. From this, we estimate that turnstones nested in coastal salt grass meadows at a density of 1.11 ± 0.16 birds·ha^{-1}; in mixed graminoid and dwarf shrub meadows at 0.75 ± 0.11 birds·ha^{-1} within 2 km of the coast and at 0.09 ± 0.03 birds·ha^{-1} farther inland; and on dwarf shrub mat tundra at very low densities of 0.04 ± 0.04 birds·ha^{-1}. Because dwarf shrub mat tundra was scarce in our samples, the estimate of density did not change when this habitat was combined with graminoid and dwarf shrub meadows (Table 4).

Population estimate for the central Yukon-Kuskokwim Delta.—The population of Black Turnstones nesting on coastal lowlands between the Askinuk Mountains and north Nelson Island (Fig. 1) was estimated at 61,000 to 99,000 birds (95% CI) with a point estimate of about 80,000 birds (Table 4). Coastal salt grass meadows supported more than a quarter of the population. About 65% of the turnstones concentrated in salt grass meadows and other habitats within 2 km of the coast. The remainder were scattered at very low densities throughout interior lowlands (Table 4).

DISCUSSION

Distribution patterns.—Our surveys clearly demonstrated that the breeding distribution of Black Turnstones on the central Yukon-Kuskokwim Delta is closely linked to the distribution of salt grass meadows. This pattern is consistent with historical museum records and with earlier published accounts. The distribution of turnstones in coastal habitats

TABLE 4

ESTIMATE OF THE SIZE OF THE NESTING POPULATION OF BLACK TURNSTONES ON COASTAL LOWLANDS OF THE CENTRAL YUKON-KUSKOKWIM DELTA BETWEEN THE ASKINUK MOUNTAINS AND NORTH NELSON ISLAND

Habitat	Area (km^2)	Estimated nesting density ($birds \cdot ha^{-1}$)[a]	Population size	
			Point estimate	95% CI
Coastal salt grass meadows	190	1.11 ± 0.159	21,000	15,000–27,000
Other habitats				
0–2 km from coast	400	0.75 ± 0.106	30,000	22,000–38,000
>2 km from coast	3245	0.09 ± 0.025	29,000	13,000–45,000
Total	3835	0.21 ± 0.025	80,000	61,000–99,000

[a] Corrected mean = mean number detected on transects · mean correction factor (0.391) derived from study plots; standard error = estimate from 100 bootstrap samples in each stratum. See Methods for details.

within Angyoyaravak Bay also mirrored that found across the entire Yukon-Kuskokwim Delta during surveys in 1979 and 1981 of breeding birds present on a sample of 65-ha plots (Yukon Delta National Wildlife Refuge [YDNWR], unpubl. data). On these surveys, turnstones were recorded on 94% of 17 plots in salt grass, graminoid, and dwarf shrub meadows, on 60% of 10 plots vegetated about equally by meadows and dwarf shrub mat tundra, and on only 33% of nine plots in dwarf shrub mat tundra. The importance of salt grass meadows to the central delta population is emphasized by the fact that this habitat supports about 25% of the breeding population but comprises only 5% of the coastal lowlands. Elsewhere throughout their range, Black Turnstones appear to be almost entirely restricted to salt grass meadows (see Murie 1959, Williamson and Peyton 1962, Wright 1979, Gill et al. 1981, Kessel 1989, Petersen et al. 1991).

There are, however, some notable exceptions to this pattern. Sparsely vegetated islands and shorelines of low relief along major rivers are used more regularly for breeding than has been previously recognized. This conclusion is supported by the inland breeding records along various active tributaries of the Yukon River, on the Kuskokwim River near Bethel, throughout Bristol Bay, and on the Utukok River in the Brooks Range. Our sighting of a turnstone on the north Yukon Delta at Emmonak (Fig. 1), along with other records, suggests that they may breed in very low densities throughout the deltaic system. During a study of avian habitats at the mouth of Uwik Slough (Fig. 1), R. D. Jones, Jr. and M. Kirchhoff (unpubl. data) recorded adults six times during June and once in July 1977. They also observed several juveniles in late summer. During

a survey of the entire north delta in June and July of 1985, turnstones were recorded seven times at four different sites within 15 km of the coast (C. Ziobran, YDNWR, unpubl. data). Twelve turnstones were also encountered from 7–29 June 1985 along a 70-km stretch of the Andreavsky River up to 90 km inland in the adjacent Nulato Hills (E. Buelna, YDNWR, unpubl. data). A single bird was sighted on the east fork of the river on 16 June 1988 (B. J. McCaffery, YDNWR, in litt.).

The reported occurrence of a small breeding population of Black Turnstones far inland along the Utukok River (Table 1; J. Hechtel, pers. comm.) constitutes a northern extension of the species' known breeding range. Because of the remoteness of this region, we do not know if their occurrence constitutes a recent pioneering effort. There are no other records north of Kotzebue Sound, either inland in neighboring mountains (Childs 1969, Dean and Chesemore 1974) or along the coast (Bailey 1948, Gill et al. 1985, W. Lehnhausen and S. Quinlan, unpubl. data).

We question two previously published breeding records at the inland and southern distributional limits (Fig. 2). The most inland record, eggs collected at Takshagemut (=Takshak Village) about 155 km inland along the Yukon River in 1868 (Gabrielson and Lincoln 1959), is probably erroneous. Based on accounts of early expeditions to this area, including William Dall's (1970) journal, we believe that the single egg set collected on the Yukon River that year was only about 60 km from the mouth of the river. The southernmost record for Chichagof Island (Abbott 1915) remains somewhat of a mystery because we were unable to locate the original egg set or any written account of the expedition. No other breeding records for southeastern Alaska exist, and there is no habitat currently considered suitable for their nesting on Chichagof Island (Webster 1986, in litt.). We consider this area to be well out of the normal breeding range for the species.

Population estimate.—Based on the available data, we estimate that about 80,000 turnstones breed on the central delta between Kokechik Bay and north Nelson Island, but this estimate may be high. We are more confident in the estimate for coastal salt grass meadows (21,000) and less confident in the estimate of numbers dispersed over interior lowland (29,000). The latter is derived from fewer samples of a much greater area. With the limited data, we had to assume that densities detected from 2–12 km inland also occurred up to 25 km inland. Dwarf shrub mat tundra, which supports extremely low densities of nesting Black Turnstones, occurs in increasing abundance inland within the zone we delineated as coastal lowlands. Since we had no accurate measure of its abundance relative to the meadows with which it is interspersed, we were not able to treat this as a separate stratum to refine our population estimate.

Given the distribution of appropriate habitats and data gleaned from museum records and other studies, we speculate that no more than about 15,000 turnstones breed in Alaska away from the central Yukon-Kuskokwim Delta. The second greatest concentration of breeding Black Turnstones probably occurs on coastal lowlands between south Nelson Island and Goodnews Bay, surrounding the Kuskokwim River mouth (Fig. 2). Overall, the turnstone world breeding population probably numbers no more than 95,000 individuals, of which about two-thirds nest within 2 km of the coast.

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SHORT COMMUNICATIONS

Characteristics of foraging perches used by breeding Bald Eagles in Montana.—Bald Eagles (*Haliaeetus leucocephalus*) spend most daylight hours perching (Steenhof et al. 1980, BioSystems Analysis 1985, Stalmaster 1987). Important attributes of a preferred perch may include proximity to potential prey, isolation from disturbance, good visibility of surrounding terrain, and accessibility for landing and departing (Stalmaster 1987). Perch use has been documented frequently for wintering and migrating Bald Eagles (e.g., Stalmaster and Newman 1979, Hansen and Bartelme 1980, Steenhof et al. 1980, Grubb and Kennedy 1982). Chester et al. (1990) described perches used by nonbreeding summer residents. There have been few studies of perch selection by nesting Bald Eagles (BioSystems Analysis 1985, Grubb et al. 1988, McGarigal et al. 1991).

During the 1985–1988 nesting seasons, we examined characteristics of foraging perches in the three active Bald Eagle breeding territories in Glacier National Park (GNP), Montana. Frequently used and potential but unused perches were compared on two levels: site and tree. We assumed that an eagle first chose an area, or site, in which to perch, and then selected a specific perch tree at that site. Johnson (1979) discussed this type of increasing specificity in habitat selection. We compared characteristics of used perches (site and tree) with available perches to determine if preference for certain perch types existed.

Study area.—GNP (48°30′N, 114°00′W) encompasses 410,200 ha. Forested areas have not been heavily impacted by logging. There were six known Bald Eagle territories in GNP during our study; each nest was within 0.5 km of an oligotrophic lake covering 360 to 2760 ha. We studied territories at Lake McDonald (2760 ha) and Logging Lake (445 ha), both near the headwaters of the Columbia River, and Waterton Lake (1347 ha), in the Hudson Bay drainage. The Lake McDonald shoreline is occupied by numerous private homes and recreational facilities, concentrated at all third order stream inlets and at the outlet. A highway borders one shore, where trees in several eagle-foraging areas were cut to provide scenic vistas. Logging Lake, 6 km from the nearest road, has minimal backcountry facilities. The U.S.–Canada border bisects Waterton Lake. A road and townsite are near the outlet, in Canada, and a visitor-use complex is situated at the Waterton River inlet in the U.S.

Predominant tree species occurring in eagle-use areas are western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), black cottonwood (*Populus trichocarpa*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), western hemlock (*Tsuga heterophylla*), and paper birch (*Betula papyrifera*) (Habeck 1970).

Methods.—During 6508 observation hours we recorded adult Bald Eagle activities, including perch locations and perch durations. Observation periods ranged from 2 to 16.5 h per day. Perches used more than twice were considered frequently used. Less frequently used perches were excluded from analyses to avoid sampling perch use that may have been incidental. Because nests were at least 300 m from lakeshores, where most foraging occurred, we excluded perches proximate to nests from analyses of foraging perches.

Designating the perch tree as the center of the perch site, we measured the distance from each perch site to the nest, main inlet, nearest lake tributary, trail, campground, and building, using a Numonics digitizer and U.S. Geological Survey 7.5′ quadrangle maps. At Waterton, the nest was associated with the second largest inlet rather than with the main inlet as at the other lakes; therefore, we also measured the distance to the "nest inlet" from each perch in the Waterton territory. At McDonald we measured distance to the lakeshore road; roads nearest to Waterton and Logging were too far (5 to 11 km) to influence observed eagle-foraging areas. We used lake depths as indices of prey (fish) availability. Using U.S. Fish

and Wildlife Service (1980) bathymetric maps, we determined depth (categorized into 6.1 m intervals) at distances of 50 and 100 m from shore nearest each perch for McDonald and Logging (not available for Waterton). We then measured all variables for 100 randomly selected control sites at each lake.

Values used in statistical analyses of perch sites were weighted by the proportion of total perching time spent at each site. We determined median and range for distance variables at perch and control sites for each territory. Spearman rank correlation (r_s) between variables for random sites at each territory were used to aid in interpreting results. Because intensity of human use varied greatly among lakes, we analyzed perch site variables separately for each territory.

We recorded six variables for each perch tree: (1) distance to shore, (2) dbh, (3) height, (4) species, (5) structure class, and (6) percent screening (percent of area between the perch and lakeshore that had vegetation ≥3 m high: 0 = 0–25%, 50 = 26–75%, 100 = 76–100%). Tree structure classes were (1) intact snags, (2) broken snags, (3) broken-top live, (4) dead-top live, and (5) totally live. Species selection may be influenced by structure and dbh; therefore, for analysis by species we divided trees into two categories by dbh: small (≤50 cm) and large (>50 cm).

Perch trees were compared with available trees by randomly selecting 10 of the identified perches in each territory and recording the same variables for the 10 trees nearest each randomly selected perch. We used these 10 nearest trees as controls to maximize the chance of sampling the group from which the perch was selected. Control trees were within the same minimum height, dbh, and maximum distance from shore as perches at the same lake. We ranked all trees (perch and controls) at each site from lowest (1) to highest (11) for height and dbh.

We used simulation to test the observed selection against a model or random selection. In the simulation, a tree was selected randomly from the perch and control trees at each site and summary statistics computed for these 30 randomly selected trees. This was repeated 25,000 times. We estimated the expected value of each summary statistic and the probability of obtaining a result as far from expected as was observed.

Results.—Eagles perched 98% of observed time. Eighty-five percent of all perches (N = 94) were at frequently used lakeshore foraging sites. Some sites received a large proportion of foraging perch use (e.g., one site at Logging had 55%). At McDonald, median distances from perch sites to nest, main inlet, building, and tributary were less than from random sites; median distances to trail, road, and campground were greater (Table 1). There were relatively large positive correlations ($r_s > 0.4$) among the first four variables; trail and campground distances were negatively correlated with these four ($-0.8 \leq r_s \leq -0.1$).

At Logging, median distances from perch sites to nest, main inlet, building, and campground were less than from random sites, and median distances to trail and tributary were nearly identical. There were large positive correlations among all variables ($r_s > 0.5$) except distance to tributary. At Waterton, median distances from perch sites to nest and nest inlet were less than from random sites, and distances to trail, tributary, main inlet and building were greater. Median distance to campground was similar for perch and random sites. Distances to nest and nest inlet were negatively correlated or nearly uncorrelated with all other variables ($-0.9 \leq r_s \leq 0.1$), and were positively correlated with one another ($r_s = 0.7$).

Lake depths near perch sites were considerably less than near random sites at McDonald and Logging ($P < 0.001$, chi-square test). Eighty-nine percent of perch times occurred at sites where lake depth 50 m from shore was shallow (<6.1 m); depth was shallow at only 57% of random sites. Seventy-eight percent of perching occurred at sites with shallow depths at 100 m from shore; depth was shallow at only 34% of random sites.

Table 1

Distances (M) from Bald Eagle Perch Sites and Random Sites at Three Nesting Territories in Glacier National Park, Montana, 1985–1988. Perch Site Values Weighted by Time Spent at Each Perch

	Territory					
	McDonald		Logging		Waterton	
Distance to[a]	Median	Range	Median	Range	Median	Range
Nest						
Perch	2290	450–4010	220	200–1820	800	450–2950
Random	2460	360–4530	880	260–2220	1670	420–2970
Tributary						
Perch	90	20–1730	160	0–580	360	20–600
Random	500	10–3840	170	10–600	170	30–710
Main Inlet						
Perch	290	80–4160	150	0–1490	2460	90–3560
Random	2480	130–5770	560	40–1910	1910	70–4500
Nest Inlet						
Perch					1030	60–3360
Random					1480	30–3400
Trail						
Perch	430	60–1290	420	10–790	1060	20–1300
Random	260	10–1110	410	0–850	200	0–1210
Campground						
Perch	2920	20–3620	250	20–1270	1520	430–2610
Random	1850	0–3870	630	30–1310	1470	40–2810
Building						
Perch	140	20–1870	400	170–1630	1540	40–2350
Random	360	0–3510	540	60–1960	1170	20–2400
Road						
Perch	280	20–780				
Random	110	0–2460				

[a] All differences between median values for perch and random sites are significant at the 0.001 level (sign test) except distance to tributary ($P = 0.76$) and trail ($P = 0.99$) at Logging Lake and distance to campground ($P = 0.92$) and building ($P = 0.002$) at Waterton Lake.

Six tree species were used as perches; most were totally live or snags (Table 2). Dbh ranged from 22 to 159 cm ($\bar{x} = 67.1 \pm$ [SD] 29.9 cm). Distance to shore varied from 0 to 60 m ($\bar{x} = 7 \pm 11.7$ m), and tree height ranged from 6.5 to 47 m ($\bar{x} = 23.8 \pm 9.8$ m).

For the 30 randomly selected perches, mean height rank was higher than the expected mean rank (six) under the random selection model ($\bar{x} = 7.3$, $P = 0.022$) for all territories combined. When analyzed separately, however, perch tree rank at McDonald was slightly lower ($\bar{x} = 5.5$, $P = 0.60$). Perch dbh ranked significantly higher than expected ($\bar{x} = 9.4$, P

TABLE 2

RELATIVE FREQUENCIES (%) OF 94 PERCH TREES AND OF A SUBSET OF 30 RANDOMLY SELECTED PERCH TREES FOR SPECIES, STRUCTURE, AND LAKESHORE SCREENING FOR THREE BALD EAGLE TERRITORIES IN GLACIER NATIONAL PARK, MONTANA, 1985–1988. EXPECTED DISTRIBUTION AND *P*-VALUE ESTIMATED UNDER RANDOM SELECTION MODEL BY SIMULATION

	94 perches	30 randomly selected perches		
Characteristic	Observed	Observed	Expected	*P*[a]
Species				
Douglas-fir	28	33	20	0.047
Black cottonwood	29	27	13	0.002
Engelmann spruce	19	17	27	0.13
Lodgepole pine	10	13	6	0.050
Western larch	11	10	8	0.67
Subalpine fir	0	0	11	0.018
Western hemlock	0	0	7	0.18
Paper birch	0	0	4	0.38
Western red cedar	0	0	3	0.52
Western white pine	4	0	2	0.65
Structure				
Snag	30	37	4	<0.001
Dead-top or broken-top, live	14	20	2	0.004
Totally live	56	43	94	<0.001
Screening				
0%	46	60	23	<0.001
50%	6	13	16	0.79
100%	24	27	61	<0.001
Unknown	23			

[a] Probability under random selection that relative frequency would be as different from expected as observed.

< 0.001). This difference persisted even after adjusting for screening and structure. Thus, the high dbh rank of perch trees cannot be explained by an association with these other variables. As mean dbh and height of all trees increased from lake to lake, difference in ranks of perches and controls decreased.

Douglas-fir, black cottonwood, and lodgepole pine were used more than expected (Table 2). All other species except western larch were used less than expected. Snags, dead-top, and broken-top live trees were used substantially more and totally live trees substantially less than expected. This pattern was consistent even when controlling for size (dbh) and species. Where totally live trees were used and other structure types were present, the perch was either a Douglas-fir or black cottonwood which was taller, had larger dbh, and/or was much closer to shore.

Within the small tree category, 13% (5/38) of snag or dead-top and 1% (2/93) of totally live trees were used. Within the large tree category, 50% (12/24) of snag or dead-top and 17% (11/63) of totally live trees were used. Among small trees, lodgepole pine was preferred.

Douglas-fir, black cottonwood, and Engelmann spruce were preferred among large trees and were the only species of totally live trees used. Unscreened trees were used substantially more than expected and fully screened trees less. Unscreened perches tended to be shorter (median height = 26.5 m for screening = 100%; median height = 27.2 m for screening = 50%; median height = 19 m for screening = 0%).

Discussion.—Distances between perches and nests were relatively short at Logging and Waterton, probably because eagles tend to locate nests near favorable foraging sites. At McDonald, human activity along much of the shore may have prevented placement of the nest near a favored foraging location (Fraser et al. 1985, Yates 1989).

Intense human use of the main inlet at Waterton excluded nesting and most perching. An average of 380 people daily visited the facilities at this location during the 1987 summer season, when most observations were made. The nest and foraging locations probably shifted to the undeveloped secondary inlet when human use of the main inlet increased several decades ago. Although intensity of human use at the main inlets of the other lakes was not quantifiable, it was much lower (pers. obs.). Distance to tributary may have been less important at Logging and Waterton, where tributaries were more abundant and all perch and random sites were close to a tributary.

Many lakes in the mountains of the western United States are oligotrophic, with low productivity and few littoral areas. Where shallows do occur, fish tend to be more concentrated, visible, and accessible to eagles. Haywood and Ohmart (1986) stressed the dependance of inland breeding Bald Eagles on benthic-feeding fish and the relationship of nest-site selection to physical characteristics of the stream bottom. McGarigal et al. (1991) also found that foraging areas on the Columbia River were associated with shallow water. Association of perch sites with relatively shallow areas of lakes was evident in our study. We believe that perch proximity to shallow water is very important at deep water lakes. Overall, the most consistent differences we found between random and perch sites were related to foraging opportunities of the site (lake depth and distance to inlet or tributary) and to distance to nest. Inconsistencies among lakes in distances from perches to human development may be due to correlations with more important variables and/or variation in type and intensity of human use at the lakes. Eagles did not seem to avoid the facilities at Logging, where there was less human activity. At McDonald and Waterton, human activity varied during the nesting season, but was intense at most facilities. Chester et al. (1990) also found inconsistencies among distances between eagle perch sites and potential sources of disturbance in North Carolina. Eagle use of developed areas was less than expected on Chesapeake Bay, and areas of human activity were used significantly less than those without such activity (Buehler et al. 1991). Bald Eagles on the Columbia River avoided favored foraging sites when boats were present (McGarigal et al. 1991).

Foraging perch selection was influenced not only by site factors, but also by tree characteristics. As mean dbh and height of available trees increased among lakes, selection for size became less important. At McDonald, perches were shorter than controls but were closer to shore than at the other lakes. This may have been related to foraging behavior at McDonald, where eagles often captured suckers (*Catostomus* spp.) in near-shore shallows. Because the locations of these fish were predictable, the most important criterion for perch selection probably was nearness to accessible food rather than the more comprehensive view afforded by a taller, more distant perch. The positive correlation between height and percent screening may indicate a wider view from, and a clearer flight path to, the smaller perch trees. Grubb and Kennedy (1982) reported a similar relationship between perch height and surrounding vegetation for wintering Bald Eagles in the Southwest.

The preference for snags and dead-top and broken-top live trees is consistent with Stalmaster and Newman (1979), Hansen and Bartelme (1980), Steenhof et al. (1980), Grubb

and Kennedy (1982), Biosystems Analysis (1985), and Fielder and Starkey (1986) who found that Bald Eagles favored snags and partly dead trees. These tree types tended to be large and open in structure, making them more desirable as perches. Chester et al. (1990) reported that eagle perch trees had more accessible perch limbs than did neighboring trees.

Black cottonwood and Douglas-fir may have been chosen for their consistently open branching structure and large size (Stalmaster and Newman 1979, Steenhof et al. 1980). Most of our observations were made when cottonwoods had leaves. Chester et al. (1990) found hardwoods were used significantly less than pines during seasons when leaves were present. Lodgepole pine had smaller than average dbh compared with all trees sampled. Due to a recent mountain pine beetle (*Dendroctanus monticolae*) outbreak, most lodgepole pines sampled (95%) were dead, probably contributing to their frequent use by eagles. Even among snags, however, lodgepole pine was preferred. Engelmann spruce was infrequently used overall, but among large live trees, it was a preferred species. Although Bald Eagles show a preference for live larch as roost trees (Crenshaw 1985), they were not used as perches in sampled sites. However, three of eight available larch snags or deadtops were used as perches. Overall, species selection was more important among totally live trees, probably because of greater structural variability.

Proximity to a food source often is the most important criterion for perch selection (Steenhof et al. 1980). Hansen and Bartelme (1980) and Fielder and Starkey (1986) suggested that availability of suitable perch types significantly influenced Bald Eagle distributions along winter foraging areas in Washington. Although eagles forage where perch selection is limited, a variety of perch types may facilitate foraging and provide alternate perches if disturbance occurs (McGarigal et al. 1991). During the nesting season, when food demands are high, the availability of preferred perch types at favored foraging sites (e.g., inlets and shallows of oligotrophic lakes) may influence territory and nest-site selection as well as nesting success.

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ELAINE L. CATON, *Montana Forest and Conservation and Experiment Station, Univ. of Montana, Missoula, Montana 59812;* B. RILEY MCCLELLAND, *School of Forestry, Univ. of Montana, Missoula, Montana 59812;* DAVID A. PATTERSON, *Dept. Mathematical Sciences, Univ. of Montana, Missoula, Montana 59812; and* RICHARD E. YATES, *Montana Forest and Conservation Experiment Station, Univ. of Montana, Missoula, Montana 59812.* (Present address ELC and REY: *Research Division, Glacier National Park, West Glacier, Montana 59936.*) *Received 1 April 1991, accepted 6 Aug. 1991.*

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Habitat use by foraging Cattle Egrets in the Mexicali Valley, Baja California.—Most studies of habitat use and foraging behavior of Cattle Egrets (*Bubulcus ibis*) have focused on investigating whether egrets benefit more by foraging in association with cattle or by foraging alone (Heatwole 1965, Dinsmore 1973, Grubb 1976, Scott 1984). The association with cattle may be sufficiently important to confine breeding to areas near cattle (Telfair 1983:48). Besides foraging in areas with cattle, Cattle Egrets have shown preferences for short vegetation sites and irrigated meadows and have exploited a variety of foods (Siegfried 1971, Fogarty and Hetrick 1973). However, only a few studies have noted the importance of field conditions (e.g., amount of moisture, whether irrigated) on habitat use by Cattle Egrets (Dusi and Dusi 1968, Platter 1976:81, Siegfried 1978, Vermeulen and Spaans 1987), but the effect of field conditions on Cattle Egret foraging-habitat selection is not well known.

In arid agricultural ecosystems dependent on frequent surface irrigation, for example, habitat preferences of foraging Cattle Egrets may be affected by the frequency and type of irrigated fields. Here, I examine (1) habitat use by foraging Cattle Egrets during the breeding season at the Mexicali Valley, Mexico, and (2) the foraging success of Cattle Egrets in alfalfa fields.

Study area and methods.—The Mexicali Valley in Baja California forms part of Water District No. 14 (30°53′ to 32°43′N, 113°50′ to 115°52′W), a subsidiary of the Colorado River (CAEMEXI 1984:9). Most of the agricultural land at the Mexicali Valley is irrigated by surface (gravity) irrigation. I studied egrets at the southern end of the valley near a mixed heronry of Cattle Egrets, Snowy Egrets (*Egretta thula*), and Great Egrets (*Casmerodius albus*). Observations on the reproductive success of egrets breeding at this heronry are reported in Mora (1991).

To assess habitat preferences, I recorded Cattle Egrets foraging in approximately 10-ha fields over an area of approximately 300 km^2 surrounding the heronry. I assumed that adult Cattle Egrets observed within this area were breeding at the heronry. I observed egrets from 06:00 to 12:00 h at different periods during the breeding seasons of 1987, 1988, and 1989, with most observations obtained in 1988. The surveys were conducted along three main routes that included most of the area. Using binoculars, Cattle Egrets were easy to see, even from long distances, from the top of a vehicle. Feeding groups were sometimes located by following flying birds. I recorded the agricultural habitat used, conditions of the habitat (e.g., whether irrigated, behind tractors, etc.), size of the feeding group, associations with other species, direction and distance from the heronry, geographic location, and time of day. Flocks were easy to observe from short distances. Egrets were considered associated with a group if they foraged within approximately 20 m or less from another egret.

To test the hypothesis that the foraging success of Cattle Egrets was greater when they foraged under irrigated conditions than when they foraged behind tractors, I observed flocks of egrets feeding in alfalfa fields along gravity-induced running-water boundaries and behind tractors in the Mexicali Valley during July 1989. A spotting scope was used to observe foraging individuals during early morning hours (06:30–11:00). For an interval of 5 min, or until the birds moved away or stopped feeding, I observed adult and juvenile Cattle Egrets actively feeding. During this interval, I counted the number of strikes followed by a swallow and the number of strikes not followed by a swallow. Individual egrets were selected from different positions in the flock or from different patches to avoid sampling the same individuals more than once.

Data were log transformed to achieve normality to meet the assumptions of linear methods (Neter et al. 1985). I therefore used geometric means and 95% confidence intervals. Analysis of variance (ANOVA) was used to determine mean differences in habitat use among and within several agricultural habitat types, as well as among field conditions. The Scheffe method of multiple comparisons was used to detect differences between means. Chi-square procedures were used to compare frequencies of flocks observed in different agricultural habitats and in different field conditions. Two-sample t-tests were used to compare feeding success between adults and juveniles, between irrigated fields and behind tractors or cutting machines, and between irrigation days (first and second) within fields. In all cases, statistical significance was set at $P < 0.05$.

Results.—There were no significant differences in habitat use patterns among years; thus I combined all the habitat use data for the statistical analysis. Cattle Egrets were generally observed foraging in flocks from two to 1600 individuals. Single foraging birds were observed occasionally (6.7% of all observations), mostly along canals or by field edges. The agricultural crops in the study area were comprised of approximately: 8% alfalfa, 3% asparagus, 2% cantaloupe, 40% cotton, 40% fallow (including recently harvested wheat fields), 5% pastures, and 2% miscellaneous (SARH, pers. comm.). On average, 15% of the fields were irrigated,

TABLE 1
AGRICULTURAL HABITATS USED BY FORAGING CATTLE EGRETS IN THE MEXICALI VALLEY, BAJA CALIFORNIA

Agricultural habitat[a]	Number of flocks	Flock size[b]	Scheffe ranking		
Alfalfa	147	39.1 (28–54)	A		
Asparagus	16	24.6 (9–66)	A	B	C
Cantaloupe	43	21.9 (12–40)	A	B	C
Fallow field	156	20.3 (15–28)		B	
Pasture	102	16.3 (11–24)		B	C
Cotton	35	8.3 (4–16)		B	C
Canals, drainages	31	6 (4–10)			C

[a] Miscellaneous fields (N = 5) are not included in the analysis.
[b] Geometric means and 95% confidence intervals. Comparisons by one-way ANOVA; means not sharing the same letter are significantly different ($P < 0.001$).

10% had operating tractors, and 75% were non-irrigated and without tractors. Most flocks (79%) were observed within a 15 km radius from the heronry. I sometimes observed individuals taking off in the direction of the heronry from as far as 35 km; thus, Cattle Egrets may have flown that far to feed. Custer and Osborn (1978) observed Cattle Egrets feed as far as 20 km from the heronry, and Telfair (1983) noted that Cattle Egrets in Texas may visit feeding areas as far as 26–32 km from the heronry.

In general, Cattle Egrets were observed foraging more frequently in irrigated than in non-irrigated fields or behind tractors (chi-square = 560, 2 df, $P < 0.001$). This preference for irrigated fields was also consistent among all the agricultural habitats (Kendall's tau, $P < 0.05$). Cattle Egrets foraged more frequently in alfalfa, pastures, and cantaloupe fields than in cotton, fallow, and asparagus fields in irrigated ($\chi^2 = 482$, 5 df, $P < 0.001$) and non-irrigated conditions ($\chi^2 = 316$, 4 df, $P < 0.001$). Cattle Egrets were seen behind tractors only when they were operating in alfalfa and fallow fields, although tractors often operated in other agricultural habitats.

The total number of flocks observed and the mean flock size of foraging Cattle Egrets in various agricultural habitats are given in Table 1. Overall, the mean number of individuals per group foraging in alfalfa fields was significantly higher ($P < 0.001$) than the mean number in flocks foraging in pastures, fallow fields, cotton, and canals but not significantly different from the mean observed in asparagus and cantaloupe fields (Table 1.) Asparagus fields were visited only while the fields were being irrigated, whereas alfalfa and cantaloupe fields were visited during various times.

When field condition was considered, the mean size of foraging flocks in irrigated fields was significantly greater ($P < 0.001$) than the mean flock size behind tractors or in non-irrigated fields (Table 2). Under irrigated conditions, egrets foraged in larger groups in alfalfa

TABLE 2

FIELD CONDITIONS OF HABITATS USED BY FORAGING CATTLE EGRETS IN THE MEXICALI VALLEY, BAJA CALIFORNIA

Field condition	Number of flocks[a]	Flock size[b]	Scheffe ranking
Irrigated	260	49.2 (41–58)	A
Behind tractors	66	15.6 (11-22)	B
Non-irrigated	178	8 (6–10)	C

[a] 6.7% of all "groups" consisted of a single individual.
[b] Geometric means and 95% confidence intervals. Comparisons by one-way ANOVA; means not sharing the same letter are significantly different ($P < 0.001$).

($\bar{x} = 107.8$, $P < 0.001$) than in pastures ($\bar{x} = 26.4$), cotton ($\bar{x} = 14.3$), cantaloupe ($\bar{x} = 31.8$), and asparagus ($\bar{x} = 24.6$). Foraging groups in irrigated alfalfa were not different in size from groups foraging in irrigated fallow fields ($\bar{x} = 78.1$). In non-irrigated fields, the mean flock size of foraging egrets varied from 7.6 to 10.3, and there were no differences among habitats, except for cotton where the number of egrets observed was lower ($\bar{x} = 2.5$, $P < 0.05$). There were no significant differences in the mean flock size of foraging egrets behind tractors in alfalfa ($\bar{x} = 17.3$) versus fallow fields ($\bar{x} = 14.1$), which were the only two crops where egrets were observed behind tractors.

Egrets foraging in flocks were mostly not associated (N = 427, 80%) with other species. When Cattle Egrets foraged with other birds (N = 53, 17%), they usually foraged in a mixed group within the same patch, mostly in irrigated fields. Under irrigated conditions, egrets also foraged closer to one another, keeping a minimum distance of 0.5 to 1 m between individuals. Cattle Egrets were seldom observed (N = 15, 3%) foraging around grazing mammals, and only in five of these occasions (0.9%) were they associated with cattle.

The foraging success of Cattle Egrets in alfalfa fields was greater ($P < 0.001$) under irrigated

TABLE 3

FORAGING SUCCESS OF CATTLE EGRETS IN ALFALFA FIELDS

Field	Day of irrigation	Individuals observed	Prey/min[a]	Scheffe ranking
1	First	19	7.2 (5.1–10.2)	A
3	First	18	7.1 (5.0–10.1)	A
	Second	30	3.5 (2.6–4.6)	B
2	First	28	5.2 (3.9–6.9)	A

[a] Geometric means. Comparisons among fields by one-way ANOVA; within fields by *t*-test. Means that do not share the same letter are significantly different ($P < 0.001$).

conditions (N = 95) than behind cutting machines (N = 25). Egrets foraging in surface-irrigated alfalfa fields by the edge of running water, captured prey at a mean rate of 5.2 prey/min, with approximately 95% of the strikes resulting in success. The mean capture rate behind cutting machines was 2.6 prey/min. Egrets foraging behind cutting machines moved more often and appeared to pursue their prey farther than in irrigated fields. The feeding success of Cattle Egrets was not significantly different among three irrigated alfalfa fields during the first day of irrigation (Table 3), but was higher ($P < 0.001$) during the first day than during the second day of irrigation within the same field (Table 3). No differences in feeding success were observed between adult and juvenile egrets in alfalfa fields, under irrigated conditions ($\bar{x} = 5.5$, and 4.7 prey/min, respectively), and behind cutting machines ($\bar{x} = 2.5$, and 3.4 prey/min).

Discussion.—Cattle Egrets at the Mexicali Valley foraged primarily in surface-irrigated agricultural areas that provided a patchy, highly concentrated, ephemeral source of insect prey. Siegfried (1978) pointed out that the expansion of Cattle Egrets in Africa occurred, not because of cattle, but because of the development of irrigation systems and more intensive farming. A similar situation may be occurring in some areas of northwest Mexico and the southwestern U.S. where surface irrigation systems are common. Wading birds in Italy fed intensively on irrigated rice fields during the breeding season and had higher foraging success in these fields than when foraging in non-agricultural habitats (Fasola 1986). Preference of wet rice fields by foraging Cattle Egrets has also been observed in north Sulawesi, Indonesia (Vermeulen and Spaans 1987).

In agricultural environments with a predominance of surface irrigation systems, Cattle Egrets may frequently choose foraging habitat based on the condition of that habitat (e.g., running water) because prey may be more easily available under these conditions. These high quality patches (irrigated fields) can be predicted since they may last for several days and Cattle Egrets are likely to make more than one feeding trip per day during the breeding season. A brief inspection of the water-soil interface shows increased insect activity at the edge of running water where crickets, grasshoppers, and spiders were readily available to the egrets. Alfalfa fields were probably favored because they were often irrigated and cut, activities which increased the number of insects available to egrets. Egrets were as common in pastures and cantaloupe fields as they were in alfalfa; however, the foraging preference for alfalfa fields was more manifest because the feeding flocks were larger in alfalfa than in pastures and cantaloupe fields, particularly under irrigated conditions.

Access to surface irrigation fields may be important for Cattle Egrets especially during the breeding season when food requirements of their young are great. Differences in feeding frequency intensity between the breeding season and the winter have been observed in other egrets (Erwin 1985). The stomach contents of Cattle Egrets collected during the winter at Mexicali showed that they had fed more on mice than during the summer when they fed mostly on insects (Mora, unpubl. data). However, it is not known whether this change in diet is due to temporal variation of prey or to a seasonal shift in prey preferences by Cattle Egrets.

The association of Cattle Egrets with grazing cattle was relatively minor at the southern part of the Mexicali Valley. Egrets may be more likely to join cattle under dry conditions (Blaker 1969) or when they forage around forests rather than around pastures (Thompson et al. 1982). Cattle Egrets may have evolved in association with grazing mammals (Siegfried 1978) but may take advantage of sudden bursts in prey availability caused by surface irrigation in agricultural ecosystems.

The greater feeding success of Cattle Egrets in surface-irrigated alfalfa fields compared to success behind cutting machines or tractors and the larger flock sizes of foraging egrets in irrigated habitats indicate that flock size and feeding success are directly correlated in Cattle

Egrets. This is further supported by the smaller flock formation and the lower feeding success of egrets when they fed in the same field during the second day of irrigation. In surface-irrigated fields, flock size and feeding rates may be determined primarily by prey density. Scott (1984) found that the feeding rates of Cattle Egrets foraging near cattle were determined by prey density and that the formation of feeding groups was determined by prey size.

Under irrigated conditions, egrets fed in very dense flocks. Cattle Egrets may be able to assess patch quality based on surface irrigation and use this information as prescient (i.e., foresighted) foragers (Valone 1991). One benefit of egrets feeding in flocks may be to gain protection against predators by reducing scanning time and allocating more time to feeding (Barnard 1980, but see Scott 1984). I observed one case of a group of Cattle Egrets mobbing a coyote (*Canis latrans*) which had approached the feeding flock in an alfalfa field. While most egrets in the flock kept foraging, the mobbing continued until the coyote was chased away.

The feeding success of Cattle Egrets diminished when they fed behind cutting machines and tractors compared with their feeding success in irrigated fields, perhaps because fewer insects were flushed by these machines than were flushed by running water. The insects flushed by cutting machines may also have been more difficult to capture than those flushed by running water. Cattle Egrets had lower rates of intake and were more likely to fight over larger prey items (mice) when feeding behind tractors and cutting machines (7 piracy cases observed) than when feeding in irrigated fields (no piracy observed).

In conclusion, the distinct preference of Cattle Egrets for alfalfa and other surface-irrigated fields and the greater foraging success Cattle Egrets enjoy in these habitats demonstrate the important role that surface-irrigated systems may have played in the possible expansion of Cattle Egret populations in this arid ecosystem.

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MIGUEL A. MORA, *Dept. of Wildlife and Fisheries Biology, Univ. of California–Davis, Davis, California 95616.* (Present address: *Dept. of Fisheries and Wildlife, Pesticide Research Center, Michigan State Univ., East Lansing, Michigan 48824.*) *Received 26 June 1991, accepted 17 Sept. 1991.*

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Seasonal dynamics of bird populations in small New England wetlands.—Wetlands are widely recognized as ecosystems with diverse attributes (Office of Technology Assessment 1984), including a distinctive avifauna (Burger 1985). Avian communities of herbaceous wetlands, although not as rich as upland forest systems, are nevertheless varied (Burger 1985) and include economically important species (Bellrose 1978, Weller 1981). Despite the perceived value of wetlands for birds, basic avian community parameters such as species richness, species composition, and population density are often poorly documented even for commonly occurring types of wetlands (but for prairie marshes see Weller and Spatcher 1965, Kantrud and Stewart 1984, Brown and Dinsmore 1986). Here we characterize the seasonal dynamics of these parameters for a northeastern wetland avifauna.

Study areas and methods.—We studied avian community dynamics from spring 1988 to winter 1989–1990 in Connecticut (8 seasons). Six sites were chosen to represent the range of small, typically human-impacted wetlands present in the state. Sites differed in extent of

open water, vegetation type, surrounding habitat, and level of disturbance, but all were relatively small, dominated by herbaceous vegetation and bordered by thickets (i.e., areas dominated by shrubs). Subjectively ranked from most to least disturbed, they are (1) State Rt. 9 and Interstate 91 interchange, Cromwell (1.0 ha): This former streamside swamp, logged in 1987, became vegetated by herbaceous graminoids, annual weeds, stump sprouts, and patches of reed (*Phragmites communis*) and cattail (*Typha latifolia*). Two shallow (1–2 m deep) ponds bordering it were constructed in 1988, increasing the total area to about 3 ha. (2) Horsebarn Hill, Storrs (0.4 ha): This marsh, with little open water, was situated in a damp, heavily grazed cow pasture. Cattail and reed canary grass (*Phalaris arundinacea*) dominated the marsh, and a copse of boxelder (*Acer negundo*), ash (*Fraxinus americana*), and multiflora rose (*Rosa multiflora*) bordered its north side. (3) Rt. 178 and 187, Bloomfield (1.1 ha): Created by bulldozers ca 1978, this marsh was traversed by a stream that was nearly dry by mid-summer. It was vegetated by reed canary grass, cattail, and purple loosestrife (*Lythrum salicaria*) and bordered by old fields and thickets of spiraea (*Spiraea* spp.), dogwoods (*Cornus* spp.), and multiflora rose. (4) Piper Brook, Newington (2.5 ha): This floodplain marsh along Piper Brook was dominated by cattail, reed canary grass, tussock sedge (*Carex stricta*), and pickerelweed (*Pontederia cordata*). It was edged by a railroad bed and recently (ca 3 yr) cutover forest dominated by tree sprouts, weedy herbs, speckled alder (*Alnus rugosa*), spiraea, and willow (*Salix* spp.). (5) Cedar Swamp, Mansfield (3.7 ha): This streamside swamp became a herbaceous marsh when road construction raised its water level in 1965. Common herbaceous plants included bulrush (*Scirpus atrovirens*), burreed (*Sparganium eurycarpum*), sedges, and cattail. It was bordered by forest, old fields, and thickets of buttonbush (*Cephalanthus occidentalis*) and speckled alder. (6) Schoolhouse Brook Park, Mansfield (0.9 ha): This 19th-century millpond, although still with open water, was silted and vegetated by cattail, reed, and tussock sedge. It was bordered by a forest and shrubby thickets of buttonbush, spiraea, and speckled alder.

Birds were studied at these sites twice each season (8 visits/site/year) on days when weather was relatively calm and there was little or no precipitation. Although logistical difficulties (e.g., construction and heavy traffic) prevented a uniform starting time, observations began 1–2 h after sunrise. During each visit, Craig counted bird species by recording all those encountered for 6 h. By counting for 6 h, locating all species present at these relatively small sites was virtually assured. Data from both counts/season were combined to produce one species list, from which we computed seasonal species richness for each site. The seasonal frequency of occurrence of individual species was computed by dividing the number of counts on which a species occurred by the total number of censuses/season (24 over 2 years).

The relative densities of small passerines, the predominant members of the avian communities at these sites, were concurrently assessed by mist netting with two pairs of ATX nets. The inner member of the pair was placed at the thicket border, and the outer member extended into the marsh interior. Net locations were changed between visits to obtain a more representative view of avian density. Density sampling lasted 5 h/visit (20 total net h/visit), and all birds captured for the first time were banded. Capture data for any particular day consisted of birds banded plus birds recaptured from a previous visit's banding but did not include same-day recaptures. Because capture rates were low, data from all four nets for both seasonal visits to a site were combined in analyses.

Based on field observations and on habitat summaries provided by DeGraff and Rudis (1987), species were categorized by principal habitat association: (1) herbaceous marsh and associated open water and mud, (2) adjacent wetland thicket, (3) upland edge or edge thicket to upland habitats, (4) interior forest, (5) field or agricultural land, (6) mosaics of the above habitats. Analyses primarily concern birds in the first two categories, i.e., those species most closely associated with wetlands.

Factorial analyses of variance were performed on species richness data. Variables entered

TABLE 1
PERCENT SEASONAL OCCURRENCE FOR THE THREE MOST COMMON MARSH AND THICKET SPECIES

Species	Winter	Spring	Summer	Fall	Mean
Marsh:					
Red-winged Blackbird (*Agelaius phoeniceus*)	29.2 (7)[a]	100 (24)	91.6 (22)	45.8 (11)	65.6 (63)
Swamp Sparrow (*Melospiza georgiana*)	8.3 (2)	54.2 (13)	58.3 (14)	83.3 (20)	51.0 (49)
Cedar Waxwing (*Bombycilla cedrorum*)	4.2 (1)	45.8 (11)	70.8 (17)	62.5 (15)	45.8 (44)
Thicket:					
Song Sparrow (*M. melodia*)	79.2 (19)	95.8 (23)	95.8 (23)	100 (24)	92.7 (89)
American Goldfinch (*Carduelis tristis*)	50.0 (12)	79.2 (19)	87.5 (21)	95.8 (23)	78.1 (75)
Common Yellowthroat (*Geothlypis trichas*)	0	75.0 (18)	75.0 (18)	37.5 (9)	47.9 (46)

[a] Percents computed by dividing censuses on which a species occurred (N, in parentheses) by the total censuses (24/season) (×100).

into the ANOVA model were sites, seasons, and habitats (marsh and thicket). For capture data, variables entered into the factorial ANOVA model were sites and seasons. In both analyses, data from the four 1988–1989 and four 1989–1990 seasons served as replicates. Before analyzing species richness and capture data, they were square root transformed to normalize distributions and stabilize variances. Comparisons between significantly different means were made with the Bonferroni test which Day and Quinn (1989) recommended as a superior multiple comparison procedure.

Results and discussion.—During eight seasons, we encountered 121 bird species at the six wetlands. Species (N) were distributed among the six categories of habitat association as follows: marsh (31), adjacent thicket (22), edge (44), forest (17), field (13), and mosaic (6). Twelve species changed their habitat association between seasons (e.g., the Canada Goose [*Branta canadensis*] nested in marshes in spring but used agricultural land in winter).

The Red-winged Blackbird (*Agelaius phoeniceus*) was the marsh species most frequent on censuses and most often netted. It was nearly ubiquitous in spring and summer, but occurred on <50% of censuses in fall and winter (Tables 1, 2). The Song Sparrow (*Melospiza melodia*) was the thicket species most often present on censuses (Table 1) and most often netted (Table 2), with a density peak occurring in fall. It was also the most abundant species in any habitat. The seasonal occurrence of predominant species in marshes and thickets is summarized in Tables 1 and 2.

Analysis of variance revealed that species richness varied between seasons ($F = 71.0$, df = 3, 48, $P < 0.001$), although spring, summer, and fall showed little difference. Winter differed significantly from all other seasons (minimum Bonferroni difference between transformed means = 0.23; Fig. 1a). Richness also differed among the six sites ($F = 18.7$, df = 5, 48, $P < 0.0001$). The minimum Bonferroni difference (0.31) showed that Horsebarn Hill had significantly fewer species than all other sites, and Cromwell was lower in richness than

TABLE 2

PERCENT CAPTURES FOR THE THREE MOST COMMONLY NETTED MARSH AND THICKET SPECIES

Species	Winter	Spring	Summer	Fall	Total
Marsh:					
Red-winged Blackbird (*Agelaius phoeniceus*)	0	13.9 (35)[a]	10.7 (27)	0	7.4 (62)
Swamp Sparrow (*Melospiza georgiana*)	0	4.8 (12)	5.9 (15)	9.9 (28)	6.6 (55)
Common Grackle (*Quiscalus quiscula*)	0	4.0 (10)	0.8 (2)	0	1.4 (12)
Thicket:					
Song Sparrow (*M. melodia*)	25.5 (12)	22.7 (57)	32.0 (81)	45.0 (127)	33.3 (277)
Gray Catbird (*Dumetella carolinensis*)	0	6.4 (16)	13.8 (35)	3.2 (9)	7.2 (60)
American Goldfinch (*Carduelis tristis*)	0	10.8 (27)	5.1 (13)	6.4 (18)	7.0 (58)
Total captures:	47	251	253	282	833

[a] Percents computed by dividing captures/season (N, in parentheses) by total captures (×100).

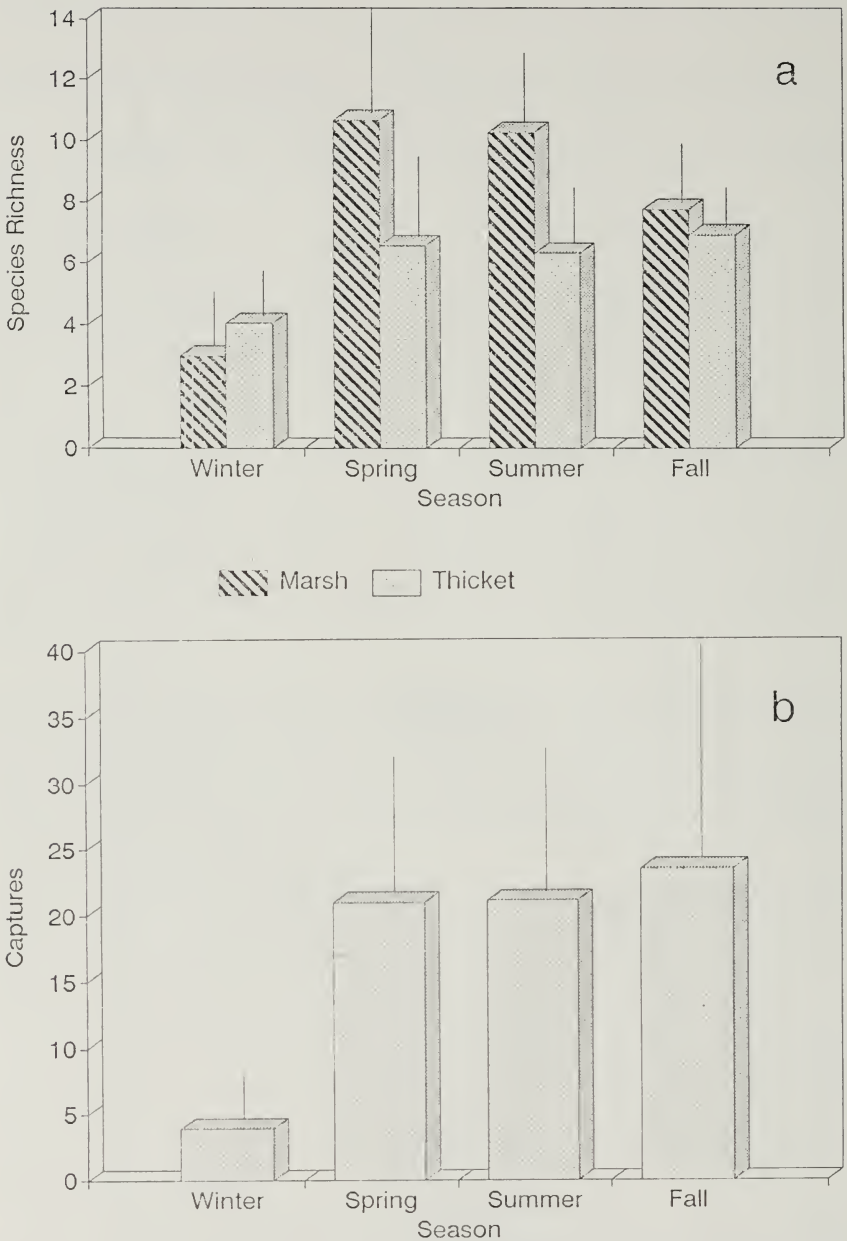

FIG. 1. Seasonal comparisons ($\bar{x} \pm$ SD) of (a) species richness, and (b) captures. N = 12 counts/season.

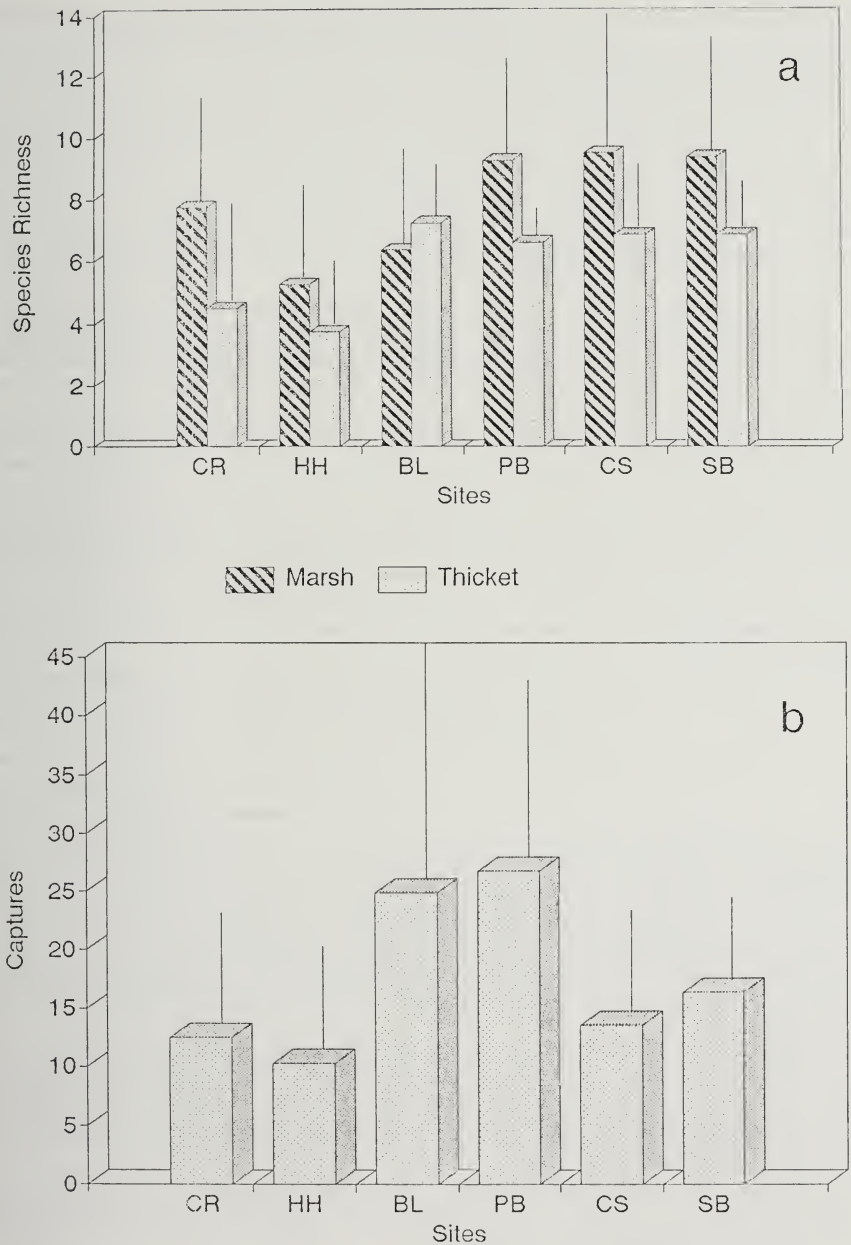

FIG. 2. Comparisons ($\bar{x} \pm$ SD) of sites and (a) species richness and (b) captures. N = 8 counts/site.

Piper Brook, Cedar Swamp, and Schoolhouse Brook, which had similarly high richness (Fig. 2a). Species richness in marshes ($\bar{x} = 7.9 \pm 3.9$) also differed from that in thickets ($\bar{x} = 6.0 \pm 2.2$; $F = 28.6$, df = 1, 48, $P < 0.0001$).

Seasonal patterns of species richness were not significantly different among sites ($F = 1.8$, df = 15, 48, $P > 0.06$) nor was the interaction of seasons, sites and habitats ($F = 0.9$, df = 15, 48, $P > 0.52$). However, sites differed between habitats in species richness ($F = 3.9$, df = 5, 48, $P < 0.005$). Marsh species were least abundant at Horsebarn Hill and Bloomfield, although Cromwell also averaged lower than the remaining three sites which were nearly uniform in marsh species richness. Horsebarn Hill and Cromwell also had relatively few thicket species, whereas the other sites were similarly high in thicket species richness (Fig. 2a).

Marshes and thickets differed among seasons in species richness ($F = 18.1$, df = 3, 48, $P < 0.001$). Although both habitats showed steep declines during winter, thickets were more uniform in richness than marshes. Marsh species outnumbered those in thickets during spring and summer, but declined to about the same number in fall. During winter, fewer species inhabited marshes than thickets (Fig. 1a).

Analysis of density data showed seasonal differences in netting frequency ($F = 23.4$, df = 3, 24, $P < 0.0001$). As with species richness, netting frequency did not differ between spring, summer, and fall, but winter was significantly lower in captures than all other seasons (minimum Bonferroni difference = 1.2; Fig. 1b). The six sites also differed in netting frequency ($F = 5.0$, df = 5, 24, $P < 0.003$); the minimum Bonferroni difference (1.6) showed that Horsebarn Hill had significantly fewer captures than Bloomfield and Piper Brook, which had the highest capture rates. Moreover, Cromwell had significantly fewer captures than Piper Brook (Fig. 2b). There was no interaction between sites and seasons ($F = 1.6$, df = 15, 24, $P > 0.15$).

Sharp declines in species richness during winter are consistent with patterns typically observed among bird communities of temperate forests (e.g., Morrison et al. 1986, Yahner 1986). However, divergent patterns of species richness for marshes and thickets indicate that these habitats function differently in their seasonal capacity to support species. Marshes reached their peak species richness in spring, when local water levels are typically high and food organisms like aquatic invertebrates are at their peak abundance (Craig 1984). As water and food levels decline through late summer (Craig 1984), progressively fewer species use this habitat. The relatively uniform species richness of thickets from spring to fall may be related to more continuously available food and cover in thickets compared to marshes.

Comparatively high capture rates from spring to fall, followed by a sharp decline in winter, further reflects seasonal patterns typically observed in temperate bird density (e.g., Morrison et al. 1986, Yahner 1986). The winter drop in species richness and density traditionally has been ascribed to the comparative environmental harshness and lack of food at this season (e.g., Welty 1982).

Although we did not attempt to quantify all physical and biotic habitat differences among sites, there was a tendency for the most disturbed sites, Cromwell and Horsebarn Hill, to have low richness and density. This suggests that disturbance negatively impacted these community parameters and points out that the role of disturbance in affecting wetland bird communities deserves further study.

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Robert J. Craig and John S. Barclay, *Dept. Natural Resources Management and Engineering, U-87, Univ. of Connecticut, Storrs, Connecticut 06269-4087.* (Present address RJC: *Northern Marianas College, P.O. Box 1250, Commonwealth No. Mariana Islands, Saipan, MP 96950*). *Received 19 Mar. 1991, accepted 8 Sept. 1991.*

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Habitat and reproductive success of Piping Plovers nesting on Great Lakes islands.— Piping Plovers (*Charadrius melodus*) historically nested along the Great Lakes. Russell (1983) estimated there may have been up to 802 breeding pairs in the Great Lakes region. In the 1940s and 1950s the Great Lakes Piping Plover population declined dramatically following shoreline development and subsequent loss of nesting habitat (Russell 1983). By 1979 the population had decreased to 38 pairs (Lambert and Ratcliff 1981). The Great Lakes Piping Plover population was listed as federally endangered in 1986 (U.S. Fish and Wildlife Service 1985). At the time of listing, only 17 breeding pairs remained in the Great Lakes population, and viable breeding areas were reduced from locations in eight Great Lakes states to sites entirely within the state of Michigan (Haig et al. 1988). The Great Lakes Piping Plover population has remained relatively stable since 1986, but in 1990 the population decreased by 35% to only 11 breeding pairs (Powell, in press). Although habitat loss may have been the primary cause of the decline in Piping Plover populations in the Great Lakes region thirty years ago, current sites used by breeding plovers are protected, and reasons for the decline in recent years are difficult to elucidate (Haig et al. 1988). The population is now extremely vulnerable and may have reached a size where natural recovery is unlikely.

Islands have historically been an important component of breeding habitat for the Great Lakes Piping Plover population. In Michigan, Piping Plovers once nested on North and South Manitou islands, North and South Fox islands, and Beaver Island (Hatt et al. 1948, Cotrille 1957). In the past decade, Piping Plovers have nested only on Beaver and High

islands (Lambert and Ratcliff 1981). Despite knowledge that Piping Plovers have historically nested at these island sites, there is a paucity of information on habitat characteristics and nesting success of island-nesting plovers in the Great Lakes (Cotrille 1957, Niemi and Davis 1979, Lambert and Ratcliff 1981, Pike 1985, Nordstrom 1990). Because of their relative isolation, these islands appear to constitute an important remnant of Piping Plover nesting habitat. The purpose of this study was to estimate the proportion of the Great Lakes Piping Plover population that uses these islands, describe nesting habitat, and estimate reproductive success.

Study area and methods.—This study was conducted on two islands in Charlevoix County, Michigan. These islands are part of the Beaver Archipelago in northern Lake Michigan. Beaver Island (45°45′N, 85°30′W), the largest island in Lake Michigan (150.2 km^2), has 67.1 km of shoreline. High Island (45°45′N, 85°40′W), 6.45 km west of Beaver Island, is 15.0 km^2 in area and has 20.2 km of shoreline (Hatt et al. 1948). Both islands are characterized by large dune systems and extensive sand beaches on their western shores. High Island includes a northeastern point approximately 1.5 km long that consists primarily of large cobble and sand. This point has been the site of a nesting colony Ring-billed Gulls (*Larus delawarensis*), Herring Gulls (*L. argentatus*), Caspian Terns (*Sterna caspia*) and, until 1989, Common Terns (*S. hirundo*). The size of the northeastern point and the width of island beaches vary from year to year with fluctuating lake levels (Cuthbert 1981).

The islands were searched systematically for Piping Plover activity by walking the beaches both along the shorelines and behind the dunes, from 15 May to 15 August, 1987, through 1990. Potential Piping Plover habitat was surveyed weekly for evidence of nesting plovers. Once courtship or territorial behavior was observed, we retreated to a distance where plovers were not disturbed and waited until they returned to a nest. Observations of Piping Plovers were then made every two to five days from a distance of at least 25 m with binoculars and spotting scopes. Piping Plover nests were not marked; natural features in the nest area were used for location cues. In 1990, predator exclosures were placed around plover nests on Beaver Island (Rimmer and Deblinger 1990). Nests were checked from one to four times a week until hatching or nest failure. After the eggs hatched, plover families were observed until the chicks fledged or disappeared. Hatching success was determined by the percentage of eggs laid that hatched. Fledging success was defined as the percentage of chicks that survived to fledging. Reproductive success was reported as the mean number of fledglings produced per nesting attempt.

Measurements of habitat characteristics around nest sites were made after the eggs hatched and the chicks had left the area, or after nest failure. Beach width was measured on calm days, from the edge of the lake to the beginning of the dune system. Dune width was measured from the rise in elevation on the lake side to the rise in elevation from the inland side of the foredunes. Measurements were not made from nests or dunes to the treeline, because in all cases the tree line was over 400 m away (Lambert and Ratcliff 1981).

Results.—Piping Plovers nested on High and Beaver islands during the four years of this study. No plovers were found on the Manitou islands, or on South Fox, Garden, Hat, Hog, Pismire, Squaw, Trout or Whiskey islands (M. Holden, National Park Service and M. J. Hamas, Central Michigan Univ., pers. comm.) (Fig. 1). Island-nesting plovers represented 14.3% of the Great Lakes Piping Plover population in 1987 (N = 2), 36.4% in 1988 (N = 4), 38.5% in 1989 (N = 5), and 25% in 1990 (N = 5).

The dune systems on the western shores of both islands are characterized by a smaller foredune located from 20 to 40 m from the lakeshore (dependent on lake water levels), a flat area behind the foredunes consisting of cobble (rounded stones <10 cm diameter) mixed with sand, and a larger dune system farther inland. The shoreline on the lake side of the foredunes is typically wide sandy beach with less than 5% vegetation and a 1–3 m wrack

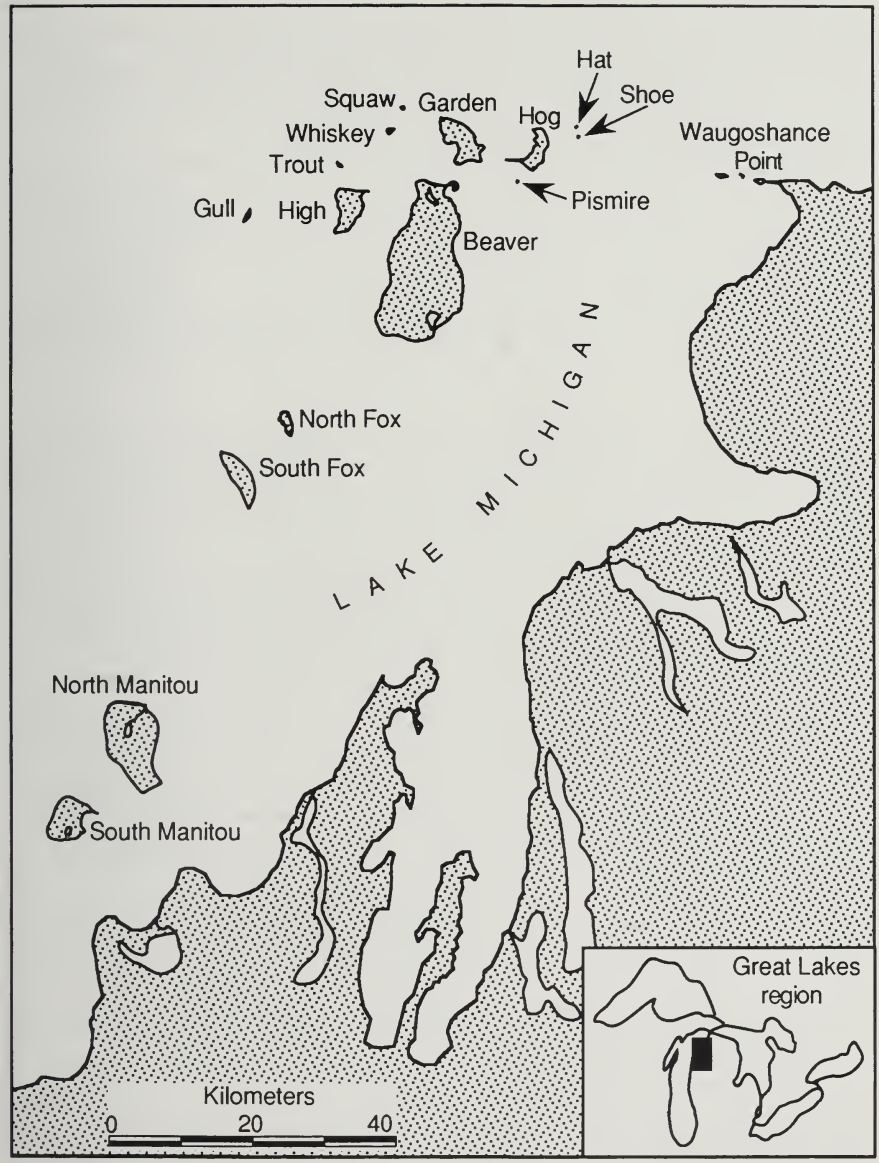

FIG. 1. Map of the islands of northern Lake Michigan. Inset shows the enlarged area in black.

line of organic debris. Small ephemeral pools with patches of sedges (*Carex* spp.) are located along these beaches on the shoreline. The vegetation on the foredunes is primarily willow (*Salix glaucopylloides*), beach grass (*Ammophila breviligulata*) and bearberry (*Arctostaphlos uva-ursi*); cover estimates ranged from 75 to 100%. The intermediate area between the dunes is patchily vegetated, with bearberry being the dominant species. A system of raised strips of cobble alternating with sand runs parallel to the foredunes.

In 1988 and 1989, a pair of Piping Plovers nested on the beach at McFadden's Point on the western shore of Beaver Island. This is state-owned property and is undeveloped and relatively undisturbed. In both years, the nest site was located on the inland side of the foredunes on a raised area of cobble surrounded by sand and sparse vegetation. In 1990, two pairs of plovers nested on Donegal Bay on the western shore of Beaver Island. This was unusual because this area has been developed with summer homes, and plovers have not nested there in over 15 years (M. J. Hamas, Central Michigan Univ., pers. comm.). Both nests were located behind the foredune in patches of cobble. One of these nests was located within 100 m of a cottage and surrounded by dunes on all other sides. The second nest was located 34 m from the road and was surrounded on three sides by cottages from 100 to 300 m distant. Both nests were provided with predator exclosures and posted as off-limits to people, dogs, and vehicles in a 50–100 m band surrounding the nest area. All four nests on Beaver Island were located behind the foredunes, with mean distances (±SD) of 69 ± 7 m to the lake and 10 ± 4 m to the dunes. Beaches at these nest sites were 34 ± 1 m wide, and dunes were 25 ± 4 m wide.

Piping Plovers nested on the western beach of High Island in all four years of this study. Five of the eight nests at this site were located behind the foredunes in cobble and sparse vegetation. Mean distances (±SD) of these nests were 87 ± 9 m from the lake and 30 ± 8 m from the dunes. Beaches at these sites were 23 ± 3 m wide, and dunes were 32 ± 5 m wide. Of the three nests on the lake side of the dune, one was destroyed during a storm when waves washed 25 m onto the beach. These nests were along the wrack line within 5 m of the foredune, 22 ± 2 m from the lake, and 4 ± 1 m from the dunes. A Piping Plover nest was located on the northeastern point of High Island in 1988 and 1989. In both years, the nest was constructed on a raised strip of cobble 150 m from the far end of the point. Two to three Herring Gull nests were located within 20 m of the nests, and from 7000 to 10,000 Ring-billed Gulls nested approximately 150 m west of the Piping Plovers.

Piping Plover chicks left the nest sites within 24 h of hatching. In cases where nests were located behind the foredune, chicks followed their parents over the dunes, through dense vegetation, to reach the lakeshore. Chicks remained on the lakeshore with one or both parents until fledging. Usually plover families remained in an area within 200 m, perpendicular to a direct line to the nest site, unless disturbed by human activity on the beach. Young plovers foraged primarily along the ephemeral pools adjacent to the shore and remained close to the vegetative cover there. Young plovers were never observed behind the foredunes after leaving the nest site.

Piping Plovers in this study were not banded. Although several of the adults nesting on the islands had been banded in the past, the bands were aluminum, and it was impossible to distinguish individual birds. However, from 1987 to 1990, a lame female nested on the western beach of High Island. This bird nested in the same general location, approximately 100 m south of the point on the beach. For two years, this individual nested behind the foredune and was successful in fledging young in 1987 and 1989. In 1988, the nest was washed out and the pair did not renest on the islands. In 1990, the lame bird was paired and was observed making a nest scrape on the lake side of the foredunes on 21 May, but was disturbed by people camping on the beach over Memorial Day weekend. This plover was next seen on the mainland at Waugoshance Point, Emmet County, Michigan, on 20 June and attempted to renest there.

TABLE 1
REPRODUCTIVE SUCCESS OF ISLAND NESTING PIPING PLOVERS FROM 1987 TO 1990

	1987	1988	1989	1990
Number of breeding pairs	2	4	5	5
Number of nests	2	3	5	3
Hatching success (%)	100	92	80	92[a]
Fledging success (%)	63	50	13	18
Number of young fledged per nest	2.5 ± 2.1[b]	1.5 ± 1.7	0.4 ± 0.9	0.7 ± 1.2

[a] Includes 2 nests with exclosures.
[b] Mean ± SD.

Reproductive success of Piping Plovers nesting on the islands was variable among years. Hatching success was high, ranging from 80% in 1989 to 100% in 1987 (Table 1). Overall reproductive success for island plovers ranged from 0.4 to 2.5 chicks fledged per nesting attempt (Table 1). In comparison, the mean number of young fledged per nest in the Great Lakes region was 1.5 ± 0.5 from 1987 to 1990 (T. Allan and R. Wolinski, unpublished data), 1.1 ± 0.6 from 1980 to 1985 at Chain of Lakes, North Dakota (Prindiville Gaines and Ryan 1988), and 0.8 ± 0.4 from 1983 to 1986 in New Jersey (Burger 1988).

Exclosures used in 1990 protected all eggs from predation. The one egg that did not hatch in 1990 was infertile. Egg failure in 1988 and 1989 was caused by storms and American Crow (*Corvus brachyrhynchos*) predation. Fledging success was much lower than hatching success and ranged from 13% to 63% (Table 1). Chick mortality was primarily due to predation, although in 1990 one 10-day-old chick disappeared after a severe storm, and three 7-day-old chicks died of exposure after their parents were killed by a Great Horned Owl (*Bubo virginianus*). In 1988 and 1989, chicks that hatched from the nest on the northeastern point of High Island were presumed eaten by gulls within two days of hatching. In both years, this nest was located within 20 m of Herring Gull nests and surrounded by loafing Ring-billed and Herring gulls. During incubation, the parents were extremely diligent, with both adults remaining within 10 m of the nests at all times. Gulls were observed walking and flying over the nest area, and were frequently chased by the adult plovers. Chicks were observed being brooded on the nest the first day of hatching but disappeared within 24 h.

Discussion.—Islands provide breeding habitat for up to 38.5% of the entire Great Lakes Piping Plover population. Beach width has been reported as an important factor for Piping Plover nesting habitat, with beaches wider than 20 m being preferred for nesting (Lambert and Ratcliff 1981, Haig et al. 1988, Prindiville Gaines and Ryan 1988). Beach width on the Great Lakes islands falls within the ranges reported for the Great Lakes and East Coast when width is measured from the water's edge to the dunes (Lambert and Ratcliff 1981, Burger 1987). However, the actual width of the beach area is much wider when the area behind the dunes is taken into account. This is important because Piping Plovers nesting on these islands tend to use habitat located on the inland side of the foredunes for nesting. Piping Plover nest surveys and habitat measurements in the Great Lakes region are often conducted on the lake side of the foredunes. The subsequent lack of information on inland habitat may lead to underestimates of habitat availability, habitat use, and population size. Although Pike (1985) reported Piping Plover nests behind the foredunes at Waugoshance Point, Michigan, they were either late nests or renesting attempts. This was not the case on the islands, where nests located behind the dunes were initiated as early as 10 May.

Faanes (1983) suggested that good visibility around the nest was an important factor in nest site selection. All of the island nests were in areas of good visibility regardless of location behind or in front of the dunes. On both Beaver and High islands, the beach area along the lakeshore is used extensively by gulls for loafing. However, gulls were never observed on the inland side of the dunes. Crows were seen occasionally in both areas but as single individuals. Both crows and gulls are known predators of Piping Plover eggs and young (Cairns 1982, MacIvor et al. 1990, Rimmer and Deblinger 1990). Location of island nests behind the foredunes may be a strategy to avoid gull predation and may account for their high hatching success.

There is evidence that Piping Plovers from the Great Plains, Great Lakes, and East Coast populations mix on the wintering ground, and there is occasional gene flow between these populations (Haig and Oring 1988a). Although natal site fidelity is generally low, Piping Plovers do return to the general area of their natal sites to breed (Wilcox 1959; Haig and Oring 1988b, 1988c; Wiens and Cuthbert 1988). Adults nesting on Great Lakes islands did return to previous nesting sites from year to year regardless of previous nest success. Despite a high mean hatching success of island Piping Plovers over the four year period, the number of young fledged per nest was similar to other studies (Cairns 1982, Burger 1988, Prindiville Gaines and Ryan 1988, Wiens and Cuthbert 1988). The number of young fledged per nest was highly variable and declined each year of the study. The causes of the low fledging success are unclear but may be due to events that affect small populations. The decline in reproductive success is coupled with a decreasing population of breeding adults in the Great Lakes Piping Plover population (Haig et al. 1988, Powell 1991). The number of young fledged each year from these islands may not be enough to maintain recruitment in an already small population. Unfortunately, survival of fledged young to breeding age and their recruitment into the Great Lakes population is unknown.

Islands are important breeding sites for Piping Plovers. Quality breeding habitat for Piping Plovers is still available on the Great Lakes islands. These areas support fewer predator species than mainland sites and have low levels of human disturbance. This is important because disturbance due to human activity has been shown to decrease reproductive success of Piping Plovers nesting along the Atlantic coast (Cairns and McLaren 1980, Flemming et al. 1988). Beach areas on the Manitou islands, Beaver Island, and High Island have been closed to human use during the Piping Plover breeding season for the past several years. Despite these factors and high hatching success of island plovers, recruitment into the Great Lakes Piping Plover population continues to decline. Piping Plover management in the Great Lakes must include alternate techniques in addition to habitat and nest protection if this population is to survive.

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ABBY N. POWELL AND FRANCESCA J. CUTHBERT, *Dept. of Fisheries and Wildlife, Univ. of Minnesota, St. Paul, Minnesota 55108.* *Received 9 April 1991, accepted 10 Sept. 1991.*

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Avian predation and parasitism on artificial nests and eggs in two fragmented landscapes.— Forest fragmentation negatively affects abundance and distribution of Neotropical migratory songbirds, in part by increasing incidences of nest predation and parasitism (Whitcomb et al. 1981, Small and Hunter 1988). Recent studies using artificial nests and eggs of domestic chickens or Japanese Quail (*Coturnix coturnix*) (Wilcove 1985, Yahner and Scott 1988) have shown greater rate of nest predation in landscapes with increasing fragmentation. Relatively high rates of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) on active bird nests also have been documented in fragmented landscapes of the Midwest (Brittingham and Temple 1983). A few experimental studies have attempted to elicit parasitism by cowbirds, but these studies were hindered by small sample size or use of eggs that were considerably larger than those of songbirds, such as eggs of Japanese Quail (Laskey 1950, Thompson and Gottfried 1981). None of these experimental studies addressed nest parasitism in relation to fragmented landscapes.

In a series of experimental studies dealing with depredation of artificial nests in forested stands of central Pennsylvania (Yahner and Cypher 1987, Yahner et al. 1989), corvids were found to have a major impact on fate of artificial avian nests. Conversely, occurrence of parasitism by cowbirds on active bird nests was uncommon in these stands (Yahner 1991). This differential effect of predation and parasitism on nesting success was not unexpected because avian nest predators may be more abundant than mammalian nest predators in forested landscapes (Angelstam 1986), and cowbirds usually are relatively low in abundance in deciduous forests of the eastern United States (Brittingham and Temple 1983).

State Game Lands (SGL) 176 in central Pennsylvania is characterized by two different landscapes, a mosaic of uncut-clearcut forested stands (Barrens Grouse Habitat [BGH] Management Area) and an intermix of forest and farmland (Toftrees Area) (Yahner and Scott 1988, Rollfinke and Yahner 1990). Thus, SGL 176 provided us with the opportunity to contrast nest predation and parasitism in distinct landscapes (see Saunders et al. 1991). We tested the hypothesis that avian predation and parasitism on artificial arboreal nests (natural nests containing artificial eggs of two color patterns) did not differ between uncut-clearcut forest and forest-farmland landscapes. In addition, we tested whether use of ceramic eggs, which simulated natural bird eggs in terms of color and size, could be used as a means of assessing avian predation and parasitism.

Study area and methods.—We conducted the study on two sites at State Game Lands (SGL) 176, Centre County, Pennsylvania. One site, the BGH Management Area, is managed for Ruffed Grouse (*Bonasa umbellus*) habitat, using an even-aged system of forest clearcutting under the supervision of the Pennsylvania Game Commission. The BGH Management Area contains 136 4-ha blocks that are divided into 1-ha (100 × 100 m) plots. Subsequent to the third cutting cycle in winters 1985–1987, 63% of the BGH Management Area was comprised of clearcut stands of three age classes, and 37% was 60- to 65-year-old forest (Yahner 1991).

The second site, the Toftrees Area, is about 10 km from the BGH Management Area and is a 450-ha intermix of approximately 50% forest and 50% farmland. Forested stands at the Toftrees Area were similar in age to those of the BGH Management Area. A portion (200 ha) of the Toftrees Area was irrigated with wastewater (chlorinated effluent) (see details in Rollfinke et al. 1990, Yahner and Morrell 1991). Overstory trees in uncut forest on both sites at SGL 176 were oak (*Quercus* spp.), aspen (*Populus* spp.), and red maple (*Acer rubrum*) (Yahner et al. 1989, Yahner and Morrell 1991).

The most common avian species nesting ≤2 m above ground at SGL 176 were Gray

Catbird (*Dumetella carolinensis*), Wood Thrush (*Hylocichla mustelina*), Golden-winged Warbler (*Vermivora chrysoptera*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Common Yellowthroat (*Geothlypis trichas*), Hooded Warbler (*Wilsonia citrina*), Indigo Bunting (*Passerina cyanea*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Field Sparrow (*Spizella pusilla*), and Black-billed Cuckoo (*Coccyzus erythrophthalmus*) (Rollfinke et al. 1990, Yahner 1991).

Natural songbird nests were collected at the two sites during late summer 1989, and each was reinforced on the outside from the base to below the rim with chicken wire painted with flat brown paint. Artificial eggs were ceramic, oval in shape (15 × 22 mm), and hand-painted either baby blue to represent a generic egg of several species, e.g., Wood Thrush or Black-billed Cuckoo, or beige with brownish specks toward one end to represent a generic egg of other species, e.g., Common Yellowthroat or Field Sparrow (Harrison 1975). We chose to use ceramic eggs in order to focus principally on avian predators which tend to be visually oriented while foraging; ceramic eggs were presumed to be unattractive as a food item to mammalian predators, which primarily use olfaction while foraging. Moreover, we assumed that ceramic eggs with comparable color and size to those of natural songbird eggs would induce parasitism by cowbirds better than larger natural chicken or quail eggs (Laskey 1950).

The study was divided into five trials from late May through June 1990, which corresponded with the timing of nest parasitism by cowbirds (Orians et al. 1989). Each trial was eight days in length. During a trial, 15 random locations were selected at interfaces of uncut and clearcut plots at the BGH Management Area and at interfaces of uncut forest and farmland at the Toftrees Area. Minimum distance between adjacent locations was 100 m, and the same location was not used in the subsequent trial.

A nest with blue eggs and a nest with brown eggs were placed at each location, giving a total of 60 nests/trial equally divided between sites and egg color (N = 300 total nests). Nests were located 5 m into uncut forest along the interface and were 20 m apart (Yahner et al. 1989). Each nest was attached 1 m above ground to the nearest woody stem (1–5 cm dbh) (Yahner and Cypher 1987). A previous study showed that predation rates of nests placed by investigators in this manner and actual nests placed by breeding birds were not different (Yahner and Voytko 1989).

We placed one egg daily (indirect host activity) in each nest for three consecutive days (days 1–3) during each trial, resulting in three eggs/nest (Thompson and Gottfried 1981). Rubber gloves and boots were worn when placing nests and eggs to minimize human scent (Nol and Brooks 1982). We determined the fate (disturbed vs undisturbed) of nests and eggs on day 2, day 3, and 5 days after placement of the third egg (day 8). Appearance of nest and eggs and mode of disturbance were used to categorize predators (Rearden 1951, Nol and Brooks 1982). A disturbed nest had ≥ one missing egg or ≥ one egg with bill marks due to pecking by an avian predator (Yahner et al. 1989). Eggs removed by predators by days 1 or 2 were replaced on the next visit to the nest. Nests and eggs were removed on day 8, and the next trial was initiated immediately.

The dependency of nest fate (disturbed vs undisturbed) on site (BGH Management Area vs Toftrees Area), egg color (blue vs brown), and trial (trials 1–5) was examined by 4-way tests-of-independence (Dixon 1985). Separate analyses were conducted for days 2, 3 and 8 (Yahner and Wright 1985). Likelihood ratios (G^2) were computed to test for interactions of nest fate with each of the three independent variables using log-linear models, which is appropriate for examining attribute variables in multi-way contingency tables (Sokal and Rohlf 1981, Dixon 1985).

Results.—Of the 300 nests, 49 (16.3%) were disturbed by day 2, 67 (22.3%) by day 3, and 172 (57.3%) by day 8 (Table 1). At least 90% of the disturbed nests had ≥ one egg removed

TABLE 1

NUMBER OF ARTIFICIAL AVIAN NESTS THAT WERE DISTURBED BY DAYS 2, 3, AND 8

Trial	Site	Egg color	No. disturbed nests		
			Day 2	Day 3	Day 8
1	BGH Management Area	Blue	4	6	9
		Brown	3	4	10
		Total	7	10	19
	Toftrees Area	Blue	0	4	13
		Brown	2	3	10
		Total	2	7	23
2	BGH Management Area	Blue	2	3	5
		Brown	3	2	11
		Total	5	5	16
	Toftrees Area	Blue	2	3	11
		Brown	5	3	10
		Total	7	6	21
3	BGH Management Area	Blue	3	4	8
		Brown	4	4	7
		Total	7	8	15
	Toftrees Area	Blue	0	4	8
		Brown	3	4	9
		Total	3	8	17
4	BGH Management Area	Blue	3	7	11
		Brown	2	1	9
		Total	5	8	20
	Toftrees Area	Blue	2	4	7
		Brown	1	3	8
		Total	3	7	15
5	BGH Management Area	Blue	4	4	8
		Brown	3	3	12
		Total	7	7	20
	Toftrees Area	Blue	2	1	4
		Brown	1	0	2
		Total	3	1	6
All	BGH Management Area	Blue	16	24	41
		Brown	15	14	49
		Total	31	38	90
	Toftrees Area	Blue	6	16	43
		Brown	12	13	39
		Total	18	29	82

from the vicinity of the nest on days 2, 3, or 8. We attributed virtually all nest disturbances to avian predators, particularly Blue Jays (*Cyanocitta cristata*) and American Crows (*Corvus brachyrhynchos*), based on nest or egg appearance (e.g., peck marks on eggs). Furthermore, several previous experimental studies in the vicinity showed that corvids were the major predator on artificial nests (e.g., Yahner and Cypher 1987, Yahner et al. 1989). Ceramic eggs also would be of no food value to predators that forage mainly via olfaction (e.g., mammals). No nests were parasitized by cowbirds.

Slightly more nests were disturbed at the BGH Management Area than at the Toftrees site by days 2, 3, and 8. However, fate of nests was dependent on site only on day 2, with 31 (20.7%) nests disturbed at the BGH Management Area compared to only 18 (12.0%) at the Toftrees Area ($G = 4.2$, df = 1, $P = 0.04$).

Slightly more nests with brown eggs were disturbed than those with blue eggs by days 2 and 8, but these relationships were not significant ($P \geq 0.43$) (Table 1). Conversely, fate of nests tended to be associated with egg color by day 3 ($G = 3.3$, df = 1, $P = 0.07$), with 40 (26.7%) nests with blue eggs disturbed versus 27 (18.0%) nests with brown eggs disturbed.

Fate of nests was not dependent on trial by days 2 and 3 ($P \geq 0.21$) (Table 1). In contrast, rate of disturbance declined over time by day 8, with 42 (70.0%) of the nests disturbed in trial 1 and only 26 (43.3%) disturbed in trial 5 ($G = 9.7$, df = 4, $P = 0.05$).

Discussion.—The rate of disturbance on artificial nests in our study (57%) was comparable to those reported in studies of nesting success of actual bird nests. For example, Yahner (1991) observed that 52% of the nests of 14 species were unsuccessful over a 3-year period at the BGH Management Area; at least 90% of the unsuccessful nests were due to avian predators (R. H. Yahner, unpubl. data). Moreover, the rate of nest disturbance in our study was similar to those noted in previous studies at the BGH Management Area, which used artificial nests (chicken wire lined with leaf litter) containing fresh brown chicken eggs (e.g., Yahner and Cypher 1987, Yahner and Scott 1988, Yahner et al. 1989). Yahner et al. (1989), in a study examining nest loss in relation to edge contrast, observed that 51% of the artificial nests placed 1.5 m above ground were disturbed. Yahner and Cypher (1987), in a study comparing nest loss among stands of different age since clearcutting, reported that 68% of the artificial nests located 0.5–1.5 m above ground were disturbed. These two studies and other previous studies (e.g., Yahner and Wright 1985, Yahner and Scott 1988, Yahner and Voytko 1989) attributed most depredation of artificial nests to corvids.

In contrast, the 57% rate of nest disturbance in our present study was considerably lower than that reported by Yahner and Morrell (1991) in a study at the Toftrees Area, which dealt with depredation of artificial nests (chicken wire lined with leaf litter) containing fresh brown chicken eggs. In the study by Yahner and Morrell (1991), 78% of the artificial nests placed at 1.5 m above ground were lost to predators. They contended that at least 90% of the disturbed nests at the Toftrees Area were due to mammalian predators, primarily raccoon (*Procyon lotor*); in most cases, these nests were destroyed within two days of placement (R. H. Yahner, pers. obs.; see also Storaas 1988). Best (1978) also reported a 78% predation rate on nests of Field Sparrows in farmlands of Iowa where mammals were major nest predators.

Differential rates of nest disturbance by avian and mammalian predators at the BGH Management Area versus the Toftrees Area were not unexpected because Blue Jays were more common at the former site, whereas raccoons were more prevalent at the latter site (Yahner and Scott 1988, Yahner and Morrell 1991). Avian nest predators often are more abundant in forested landscapes (e.g., BGH Management Area), whereas mammalian nest predators generally predominate in forest-farmland landscapes (e.g., Toftrees Area) (Angelstam 1986, Yahner and Scott 1988, Yahner and Morrell 1991).

We partially attribute the greater rate of nest disturbance at the BGH Management Area than at the Toftrees Area on day 2 to higher densities of Blue Jays in forested stands at the former site than the latter site (Yahner 1986, Rollfinke and Yahner 1990). Furthermore, a significantly greater susceptibility of nests with blue eggs by day 3 compared to nests with brown eggs at both sites combined perhaps occurred because blue eggs were more conspicuous than brown eggs to corvids which rely primarily on vision while foraging (Yahner and Wright 1985).

Previous studies, using artificial nests with brown chicken eggs at SGL 176, showed that rates of nest disturbance either did not vary among trials (Yahner and Scott 1988, Yahner et al. 1989, Yahner and Voytko 1989, Yahner and Morrell 1991) or declined over time (Yahner and Wright 1985, Yahner and Cypher 1987). The decline in rates observed in the latter two studies was attributed to the social behavior of American Crows in mid-summer. In mid-summer, crows probably fledged young and moved away from wooded areas at SGL 176 to more distant communal roosting sites and agricultural feeding areas, thereby reducing their impact on avian nests (Cross 1946, Yahner and Wright 1985, Yahner and Cypher 1987). Perhaps this behavior of crows may have explained partially lower rates of disturbance over time in our study. Another factor that may have contributed to reduced rates of disturbance in our study over time was that corvids eventually learned that artificial (ceramic) eggs were of no food value and, hence, avoided this food source (Krebs 1978). However, rates of disturbance may not have declined over time if eggs were of some food value.

Abundance of Brown-headed Cowbirds was similar at the BGH Management and Toftrees areas, despite marked differences in the landscape of these two sites (Yahner 1986, Rollfinke and Yahner 1990). Abundance of cowbirds on our sites was lower than at sites in the Midwest where 48% of the active bird nests were parasitized by cowbirds (Brittingham and Temple 1983). In contrast, only three (3%) of 95 active avian nests were parasitized over a three-year period at the BGH Management Area (Yahner 1991).

Thompson and Gottfried (1976) did not observe parasitism by cowbirds on 159 experimental nests containing two eggs of Japanese Quail; they suspected that this was due to the large size of quail eggs. In a later study, Thompson and Gottfried (1981) artificially placed three House Sparrow (*Passer domesticus*) eggs in each of 50 abandoned nests. In 25 of these nests, the three eggs were placed on the same day; in the remaining 25 nests, one egg was placed on each of three consecutive days. None and one (4%) of the nests in these first and second groups, respectively, were parasitized. In contrast, Thompson and Gottfried (1981) reported that five (23%) of 22 active bird nests in the vicinity of the abandoned nests were parasitized. They concluded that indirect evidence of host activity via daily placement of eggs by an investigator can elicit parasitism by cowbirds, but that their studies lacked a sufficient sample size to determine if parasitism of nests without direct host activity at nests (Rothstein 1976) frequently occurs. Recently Freeman et al. (1990) found that 28 (22%) of the 30 incidences of cowbird parasitism on nests of Red-winged Blackbirds (*Agelaius phoeniceus*) occurred on inactive nests, which represented a high rate of parasitism despite the lack of host activity.

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RICHARD H. YAHNER AND COLLEEN A. DELONG, *School of Forest Resources and Graduate Program in Ecology, The Pennsylvania State Univ., University Park, Pennsylvania 16802.* *Received 16 May 1991, accepted 1 Sept. 1991.*

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Notes on the breeding and reproductive biology of the Helmeted Manakin.—The Helmeted Manakin (*Antilophia galeata*: Pipridae) is a monotypic species with a mating system and distribution that may be atypical for a sexually dichromatic manakin (Marini and Cavalcanti, unpubl. data). The range (tableland of central and southern Brazil, from Maranhão and Piauí, south to Paraná, north of Mato Grosso do Sul, northeast of Paraguay [Meyer de Schauensee 1970] and also in Ceará, Brazil [P. T. Z. Antas, pers. comm.] and in extreme eastern Bolivia [Bates et al., in press]) and habitat (gallery forests in the "cerrado" region of central Brazil) are unique among manakins. In addition, Sick (1967) considered its call sonorous and "rather different from other manakins, but similar to some cotingas." Females are olive green, and adult males are black with a red crown, neck and upper back. Subadult males have green plumage mixed with black and red feathers. Immature males are similar to females. The nest and eggs were described by Ihering (1900, 1902). Since then nothing has been published about the Helmeted Manakin's natural history. The Helmeted Manakin taxonomic status is uncertain because little is known about its biology. The objective of this paper is to provide data on the Helmeted Manakin's breeding biology that may lead to a better understanding of its classification.

Study area.—This study was conducted in the gallery forest of the Córrego Capetinga (a creek) at the Ecological Station of the University of Brasília, Brasília, Distrito Federal, Brazil (15°58′S; 47°56′W). The gallery forests consist of ribbons of evergreen trees along water courses, with the tallest trees between 20 and 30 m, surrounded by natural semi-open grasslands ("cerrado"). The gallery forest studied has at least 120 species of plants, of which 76 are trees or big shrubs (Ratter 1980). Detailed information on the study area and region are in Ratter (1980), Eiten (1984), and Marini (1989).

Methods.—Nests and testes of collected birds were measured with a metal caliper accurate to 0.1 mm. Observations were made mostly in the morning (06:30–13:00) from April 1988 to March 1989. Song intensity (number of male songs/h) and chase frequency (number of chases/h) were quantified on a 2.5-ha plot, marked by a grid of 34 points at 30 m intervals. Only males under sight were sampled. The results are the combined observations of four adult males and three subadult males color banded in the study plot. Searching for birds lasted 5 min at each point with a 2–3 min interval between points. The number of hours of searching is the sum of 5 min searching periods. I visited each point approximately 41 times, totaling 117.1 hours of searching during the 12-month period of study. I made 450 sightings which lasted from a few seconds to 5 min.

TABLE 1
MEASUREMENTS OF HELMETED MANAKIN NESTS

Measurement[a]	Nest A	Nest B
Height of nest above ground	10	0.5
Outside diameter	7.5	8.4
Inside length	5.5	6.2
Inside width	5.5	5.2
Outside height	3.5	4.2
Inside depth from top of upper twig	4.0	3.4
Smallest distances of nest from the	7.2	5.4
fork along different twigs	7.5	5.7
Twig diameter before the fork	0.9	0.5
Twig diameter after the fork	0.55	0.3

[a] Measurements in cm, except for height of nest (in m).

Male testis volume was estimated from 29 birds collected in nearby gallery forests, using the formula for the volume of an ellipsoid: $V = 4/3\ \pi\ ab^2$, where a was half the length of the testis and b the radius at its widest point. I recorded molt presence or absence for the wing, tail, and body feathers from 142 individuals mist netted, collected, or from the collections of the Museu Paraense Emílio Goeldi (Belém, Pará) and the Zoology Laboratory of the University of Brasília (Brasília, DF). Banded individuals mist netted in different months were considered as a separate record for molt.

Results.—Two nests were found, one on 20 September (nest A) and the other on 9 October 1988 (B). Nest A was in late construction: it already had a well defined shape, and the bottom was almost closed. It was 10 m high near the tip of a branch, 3.6 m from the trunk, in a 15-m *Amaioua guianensis* (Rubiaceae) tree. This tree was in the center of the forest, 75 m from the creek and 90 m from the closest forest border. The nest was a shallow bowl hanging between two twigs of a fork, made of fine twigs, roots, and leaves, with a hanging leaf on the outside wall (measurements in Table 1). A green bird (probably female) used its bill and feet to arrange the nest and lining. The bird made small and slow rotating movements while sitting in the nest. On 26 September the nest was observed from 06:21 to 06:49 h with the female present for 20 of the 28 min. In the same day a male sang for 30 seconds in a tree 5 m away from the nest. The female was sitting in the nest during visits on 8, 10, 11 and 13 October, always in the same position with the head across one of the twigs. On 13 October I climbed the tree and could see two beige eggs with dark spots. No activity was observed on or after 26 October, so the fate of the nest is unknown.

Nest B, found by J. C. Motta, Jr., was similar to nest A (Table 1) and contained two nestlings with very short feathers. It was 0.5 m high in a 1-m *Miconia hirtella* (Melastomataceae) shrub along a stream border. By 11 October, one of the nestlings had disappeared, and by 13 October, the plumage of the remaining nestling was thicker. When I approached the nest on 15 October, the nestling flew away, even though its remiges were only half grown and the retrices very short. A green individual (probably female) flew from the nest in two of my four visits, and once it called ("qua" notes) and flew from perch to perch about 5 m from the nest, in an apparent distraction display. Both nests were free of feces and seeds, which were found frequently on the forest floor below the nest.

Ten females mist netted in the study area and collected in other gallery forests close to the study area had brood patches between September and December. Two collected in October and November 1988 had eggs in formation. Adult males showed more developed

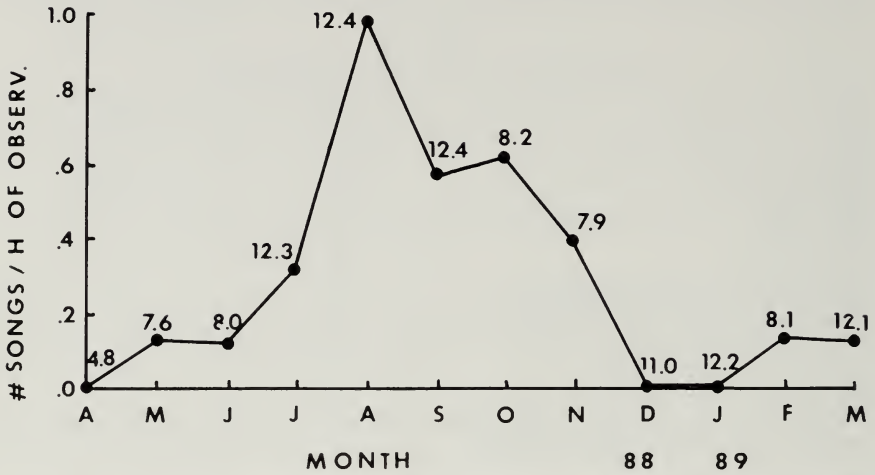

FIG. 1. Combined annual variation in song intensity of four adult males and one subadult male Helmeted Manakin. Numbers indicate hours of observation.

testes from July to December ($\bar{x}$ = 19.6 mm³, range = 4.6–39.5, N = 8) than from January to June ($\bar{x}$ = 2.0 mm³, range = 0.4–4.5, N = 9). The annual average testis size of 17 adult males, four subadult males and eight immature males were, respectively, 10.3 mm³ (range = 0.4–39.5), 6.7 mm³ (range = 0.9–13.0), and 3.7 mm³ (range = 0.3–8.9). Histological analyses of the testes of two adult males collected in October (testis size = 9.1 mm³) and December (testis size = 17.9 mm³), and two subadult males collected in October (testis size = 13.0 mm³) and November (testis size not available) showed no apparent differences. All had sperm packages and sperm in the lumina of the seminiferous tubules. No immature male testes were examined.

Adult and subadult males sing and perform circular chase flights when interacting with others in certain central areas (possible territories). Adult males often chased other adult males, but rarely chased subadult males. Although the males sing during the whole year, song intensity was higher between July and November, with a peak in August (Fig. 1). The song is a loud piercing whistle of eight notes audible from distances of at least 100 m. Songs between July and November were strong and complete, whereas songs at other times of the year were frequently weak and incomplete.

Chase frequency varied through the year. Chases consisted of at least one circular silent flight around the forest at heights varying from the understory to the canopy, and rarely involved physical contact. Occasionally the chaser pecked the back of the chased bird. Chases were most common in September (6 chases seen in 12.4 h of observation), but also occurred in August (3 chases in 12.4 h), November (2 chases in 7.9 h), June (1 chase in 8.0 h) and March (1 chase in 12.4 h). Ten of these 13 chases were between two adult males, two between an adult male and a subadult male, and one between a subadult male and a green bird. Nine of the 12 chases involving at least one adult male were inside an adult male's central area, and three were on the border of an adult male home range. Besides these 13 chases, I also saw during a mist-netting day two green birds chasing each other on a circular flight, and twice I saw a green bird chasing a subadult male for 1–2 sec on a non-circular flight.

The most intense molt period for both sexes overlaps little with the reproductive period,

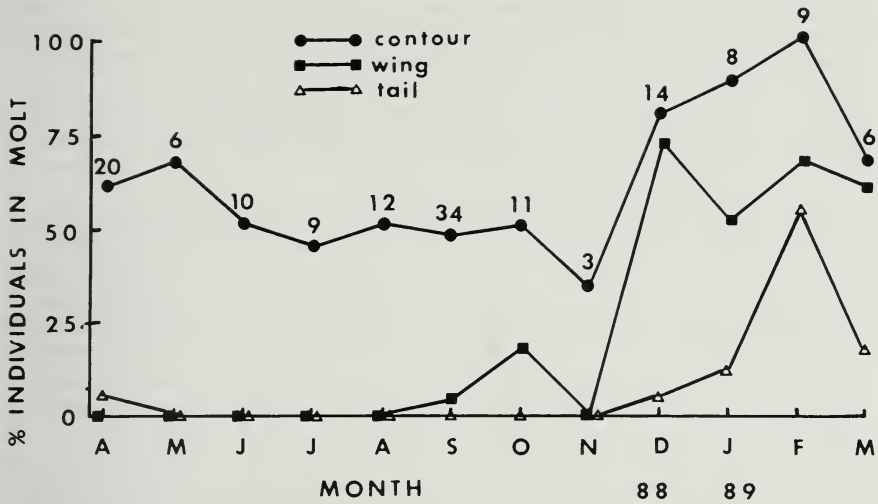

FIG. 2. Annual variation (% of individuals) in molt of wing, tail and contour feathers in the Helmeted Manakin. Numbers indicate sample sizes.

occurring from December to March, with the peak in February (Fig. 2). Body molt was recorded throughout the year, being more intense between December and February. Wing molt occurs between September and March, reaching a peak between December and March. The tail molts between December and April, reaching a peak in February.

Discussion.—Nest building (as was observed in nest A) and care of nestling (as was observed in nest B) seems to be a female activity because no male was observed close to either nest. P. T. Z. Antas (pers. comm.) observed an adult male following a female while she was carrying nest material, but also never observed a male directly engaged in nesting activities. Skutch (1949) observed only females of Red-capped Manakin (*Pipra mentalis*) working at the nest and Skutch (1969) observed only females of Blue-crowned Manakin (*P. coronata*) working at the nest and incubating. Worthington (1982) and Skutch (1969) observed females of the Golden-collared Manakin (*Manacus vitellinus*) working at the nest.

Both nests were similar to one described by Ihering (1902), which were bowl-shaped, suspended between two twigs, built of small rootlets and twigs, and lined with "vegetable horse hair" (fungal hyphae) with leaves hanging outside. The nest described by Ihering (1902) was found in December, one m above a stream, similar to the location of nest B, but not of nest A. Nest architecture is similar to other manakins (Ihering 1902; Skutch 1949, 1969; Foster 1976) and different from problematic non-manakins such as *Schiffornis* spp. (Skutch 1969).

The two eggs found in October by Ihering (1900) were described as "yellowish-white with several stripes and darker spots forming a large crown at the blunt end." The eggs observed in nest A, were similar except that stripes were lacking. Another nest found in October (P. T. Z. Antas, pers. comm.) also contained two eggs, was between 5 and 6 m high and also had a dry leaf suspended in its external wall.

Both nests observed were clean of seeds, feces, and egg shells, possibly due to cleaning of the nest by the female and/or by the nestling and the female defecating outside the nest. Foster (1976) observed that young of the Long-tailed Manakin (*Chiroxiphia linearis*) re-

gurgitated seeds and defecated in the nest. However, she found no seeds on the ground under the nest, and the nests were always clean. She suggested that females remove seeds from the nest, probably at the same time as the fecal sacs. Snow (1962) observed that the nest of White-bearded Manakin (*Manacus manacus*) with nestlings may contain feces or seeds, but the female swallows the seeds or feces or carries them away from the nest. He observed that nestlings defecate outside the nest. Also, Skutch (1949) stated that the Red-capped Manakin throws seeds outside the nest when it is incubating, and that in the nest the Blue-crowned Manakin (Skutch 1969) swallows nestlings' droppings.

The gonadal development of the males showed a pattern similar to that of the Long-tailed Manakin but different from that of the Swallow-tailed Manakin (*Chiroxiphia caudata*) (Foster 1987). The testes of immature Helmeted Manakin males are not as enlarged as the subadult male testes, which are not as enlarged as adult male testes. The testes of subadult and immature Helmeted Manakin males, like the testes of the Long-tailed Manakin (Foster 1987), are not as enlarged as the males of respective age classes of the Swallow-tailed Manakin studied by Foster (1987). Immature males, which have very small testes, do not engage in reproductive behavior, whereas subadult males, which have intermediate testes, at least occasionally sing and defend central areas like adult males (Marini 1989).

Wing and tail molt are concentrated between December and March, with little overlap with the breeding season when the energetic costs of reproduction are high. Levey (1988) observed Red-capped and White-collared manakins (*Manacus candei*) molt contour feather throughout the year and molt the wing and tail after the reproductive peak, a pattern similar to that of the Helmeted Manakin.

The reproductive period of the males (defined by gonadal development, song intensity, and male-male chase intensity) apparently began in July, reached a peak in August–September, and ended in December. The females' reproductive period (defined by nesting activity, brood patches and gonads), apparently began in August, was most intense from September to November, and ended in December. The Helmeted Manakin breeding period is similar to that of the typical breeding season of birds of the region (R. B. Cavalcanti, pers. comm.). The rainy season begins in September and ends in March–April, which means that the reproductive peak was in the first half of the rainy season and the molt peak was in the second half. Seasonal patterns of fruit abundance are not known, but presence of insects in the rainy season may also influence nesting/molt.

The Helmeted Manakin showed similarities to other manakins in nesting biology, nest architecture, male gonadal development, and molting pattern. All these observations support the present taxonomic position of the Helmeted Manakin in the family Pipridae, as has recently been supported by syringeal analysis (Prum 1989), and foraging and diet observations even though it has a unique range and may not be promiscuous.

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Miguel Â. Marini, *Dept. de Ecologia, Univ. de Brasília, Brasília, DF, Brazil 70910.* (Present address: *Dept. Ecology, Ethology and Evolution, Univ. of Illinois, Champaign, Illinois 61820.*)
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Rediscovery of the Bolivian Recurvebill with notes on other little-known species of the Bolivian Andes.—During a survey of birds in the upper Río Saguayo valley of Amboró National Park, Dpto. Santa Cruz (approx. Lat. 17°50′S, Long. 63°39′W; Fig. 1), we found populations of two little-known bird species, the Bolivian Recurvebill (*Simoxenops striatus*) and Ashy Antwren (*Myrmotherula grisea*). These species are known from only a few forest localities at 600–1400 m on the lower slopes of the Bolivian Andes in the Departments of La Paz, Cochabamba, and Santa Cruz (Remsen and Traylor 1989; this paper). The area we surveyed has been the focus of field research on the rare Horned Curassow (*Pauxi unicornis*; Cox and Clarke 1988). As detailed by Cox and Clarke (1988), Amboró National Park lies southeast of the town of Buena Vista, Dpto. Santa Cruz. The 180,000-ha park's borders are the Río Yapacaní to the west, the Río Surutú to the east, and latitude 17°51′S to the south. The southern two-thirds of this triangle is a section of the eastern foothills of the Andes ranging up to 2000 m elevation. From 16–19 August 1989, we studied resident

forest bird species in tall montane forests at ca 700–900 m on steep slopes above the upper Río Saguayo, one of the largest drainages entirely within the park. Parker documented records herein with tape-recordings of vocalizations, now housed in the Library of Natural Sounds, Cornell Univ. (LNS).

Bolivian Recurvebill.—This species was known from four specimens collected by Melbourne A. Carriker, Jr., in the 1930s (Fig. 1), two from Santa Ana, Dpto. La Paz (Carriker 1935; 15°50′S, 67°36′W), and two from Palmar, Dpto. Cochabamba (Bond and Meyer de Schauensee 1941; 17°06′S, 65°29′W, latitudes and longitudes from Paynter et al. 1975), at elevations of 670–800 m (Vaurie 1980). We observed at least four different recurvebills each day of our stay in the area. Two single birds were heard and glimpsed in very dense, shrubby vegetation (1–3 m tall) covering natural landslides on the opposite sides of a narrow, deep side canyon at an elevation of 800 m. A third individual was heard in dense, tangled undergrowth at the edge of the Río Saguayo at 700 m. These single individuals always were observed 0.5–2 m above ground in impenetrable shrubby tangles, often in the vicinity of fallen trees. In contrast to these single birds was a pair that foraged in the upper middlestory on the slopes of the main canyon. This pair was regularly associated with a large mixed-species flock, most of whose members moved through the lower canopy (above the upper middlestory) of forest at 800 m. The pair was studied for up to an hour each day, as they foraged in vine tangles from 12 to 20 m above the ground. Although difficult to see as they moved through dark vegetation, they hopped along and up vines and pecked at rotting branches and palm fronds trapped in tangles; they also probed large bromeliads, epiphytic ferns, and *Philodendron* spp. on trunks or large limbs. The large flock of canopy insectivores included pairs and/or families of the following species: White-throated Woodpecker (*Piculus leucolaemus*), Ocellated Woodcreeper (*Xiphorhynchus ocellatus*), Rufous-rumped Foliage-gleaner (*Philydor erythrocercus*), Ashy Antwren, Slaty-capped Flycatcher (*Leptopogon superciliaris*), Marble-faced Bristle-Tyrant (*Phylloscartes ophthalmicus*), Tawny-crowned Greenlet (*Hylophilus ochraceiceps*), White-shouldered Tanager (*Tachyphonus luctuosus*), Paradise Tanager (*Tangara chilensis*), Bay-headed Tanager (*T. gyrola*), and Green-and-gold Tanager (*T. schrankii*). The song of *S. striatus* is a rattling, rising series about 3 sec long that is very similar to that of the Peruvian Recurvebill (*S. ucayalae*) in pattern and quality (Parker, pers. obs.; LNS). The raspy calls ("*chet*") are also like those of *ucayalae,* but a harsh, nasal scold note ("*naah*") given by *striatus* may be unique to the species. Although these taxa are vocally similar, morphological and ecological differences suggest that they should continue to be treated as separate species. *S. striatus* apparently occurs only within a narrow elevational range (650 to 1000 m) in lower montane forests in northern Bolivia, whereas *S. ucayalae* is almost entirely restricted to extensive thickets of spiny *Guadua* bamboo in foothill and lowland forests to the north (Parker 1982, Parker and Remsen 1987).

Ashy Antwren.—Other than brief observations reported by Remsen et al. (1982), this seemingly rare species is almost unknown in life. Of the 14 known specimens, those with good locality data were collected in tall, lower montane forests from ca 600–1400 m (Remsen et al. 1982). Two pairs were observed daily with middlestory and lower canopy mixed-species flocks below camp (at 650–800 m), and a solitary male was seen by Bates and Cox in stunted, ridgetop forest above camp at ca 1000 m. The pairs were always noted with pairs of Tawny-crowned Greenlets (*Hylophilus ochraceiceps*) and were often with Golden-crowned Warblers (*Basileuterus culicivorus*) and Red-crowned Ant-Tanagers (*Habia rubica*). The antwrens primarily searched clusters of dead leaves that hung from open, slender branches, or were trapped in vine tangles, from ca 6–15 m (mainly at 12–14 m) above the ground; they also occasionally probed balls of moss on branches. They appeared to scan briefly green leaves as well but were not seen to take any prey from them. A pair, with both birds carrying green orthopterans 2 cm long, was observed on 17 August in open undergrowth

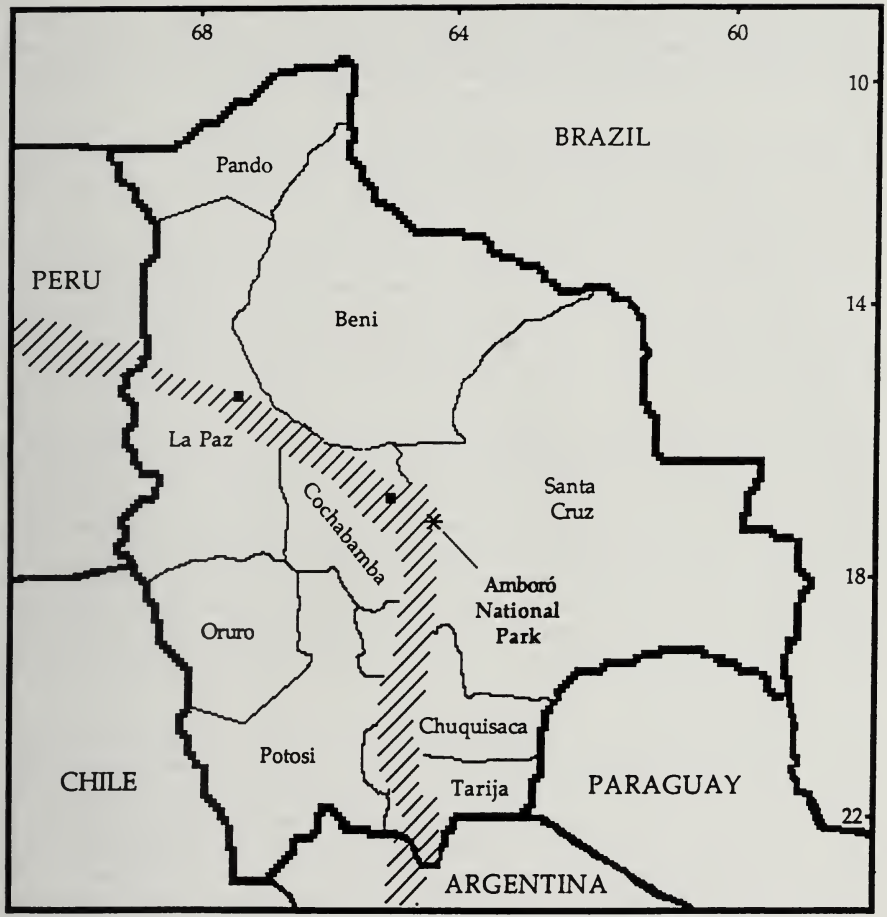

FIG. 1. The three known localities of the Bolivian Recurvebill in the eastern foothills of the Bolivian Andes. Squares refer to two sites where the species was collected by Carriker (see text). All three localities are at elevations between 670–1000 m. The shaded area approximates the eastern foothills of the Andes. Latitudes and longitudes are given on the borders of the figure.

2 m above the ground, but we could not locate a nest or young. The species reminded us of the Gray Antwren (*M. menetriesii*) in appearance (but *M. grisea* has a noticeably longer tail) and calls, which include an emphatic "*whit*" or "*wheet*" note, and twittering phrases often given by both sexes simultaneously (LNS). Males and females flicked their wings constantly, and one male occasionally flicked its tail down as it called excitedly in response to playbacks of calls. *Myrmotherula grisea* apparently occurs in tall forests within a narrow elevational zone, perhaps mainly on interior ridges, above the normal elevational limits of their more widespread congeners, White-flanked Antwren (*M. axillaris*) and *M. menetriesii,*

which were not found along the upper Río Saguayo. Recent allozymic studies of *Myrmotherula* by Hackett and Rosenberg (1990) placed *M. grisea* near Slaty Antwren (*M. schisticolor*) and Plain-winged Antwren (*M. behni*) and away from other "gray" antwrens. Like *M. grisea,* both of these species also occur in elevational zones above congeners (Hilty and Brown 1986).

Additional records for the Department of Santa Cruz.—Black-and-chestnut Eagle (*Oroaetus isidori*).—An adult circling low over forest at ca 900 m on 17 August represents the southernmost record for the Bolivian Andes, although the species occurs in montane forests in northwestern Argentina (Stresemann and Amadon 1979).

Band-bellied Owl (*Pulsatrix melanota*).—At least two pairs held territories in tall forest on the upper slopes of the valley at ca 800 m; these were vocal (LNS) just before dawn, at dusk, and sporadically through the night. This owl has been reported from Bolivia only twice (Todd 1947, Remsen and Traylor 1989) but is probably widespread in the Andean foothills (occurring as high as 1650 m, Serranía de Bellavista, Dpto. La Paz; Remsen and Parker, unpubl. data).

Andean Pygmy-Owl (*Glaucidium jardinii*).—Two or three different birds called (LNS) regularly at dawn and dusk, and occasionally at other times, day and night, in forest above camp and on a nearby ridge, ca 900–1100 m. This is the first report of this species from south of Dpto. Cochabamba in Bolivia (Remsen and Traylor 1989); however, recent records from northwestern Argentina (Prov. Jujuy and Tucumán, Straneck et al. 1987) suggest that it occurs in humid Andean forests in Bolivia south of Dpto. Santa Cruz.

Lyre-tailed Nightjar (*Uropsalis lyra*).—At dawn on 17 August, Parker heard the unmistakable flight songs of this species over the cliffs at ca 1000 m opposite camp. The only other Bolivian records were reported by Remsen and Ridgely (1980) and Remsen and Traylor (1983). The species apparently occurs all along the eastern slopes of the Bolivian Andes, from Dpto. La Paz to Dpto. Tarija.

Rufous-rumped Foliage-gleaner (*Philydor erythrocercus ochrogaster*).—One to several pairs of this montane form of *P. erythrocercus* were observed each day with mixed-species flocks (regular associates are listed under *Simoxenops striatus*) in the lower canopy of tall forest, from ca 700 to 850 m. They hopped along branches and vines near trunks of medium-sized or large trees, from 6 to 30 m above the ground; they turned from side to side to "look under" branches and probed mosses, lichens, and bark crevices. They occasionally probed in curled, dead leaves, and one hung on and scanned the underside of a live palm frond. To our knowledge, this is the first record of this distinctive subspecies for Dpto. Santa Cruz. The relationship of *P. e. ochrogaster* to other subspecies of the *P. erythrocercus* complex is unclear (Zimmer 1935). In southern Peru and Bolivia, *P. e. ochrogaster* replaces the lowland *P. e. lyra* in montane forests above ca 800 m, and ranges as high as 1650 m (Remsen and Parker, unpubl. data). However, songs and calls of *P. e. ochrogaster* recorded along the upper Río Saguayo are very similar to those of *lyra* and are more similar than one would expect if two biological species were involved. Typical songs of both forms consist of a high-pitched series of 6–7 scratchy notes that drop slightly towards the end; their call is a loud twittering note. Other similar-looking, allopatric *Philydor* species (e.g., *P. pyrrhodes/P. dimidiatus* and *P. erythrocercus/P. lichtensteini*) have very different voices (Parker, pers. obs.). On the other hand, no intergrades between *P. e. ochrogaster* and *P. e. lyra* specimens are known from the 500+ km where their altitudinally separated ranges abut.

Marble-faced Bristle-Tyrant (*Phylloscartes ophthalmicus ottonis*).—Several pairs were noted daily with upper middlestory canopy flocks at ca 800–900 m; birds behaved in manners previously described for this species (Remsen 1984, Hilty and Brown 1986). Individuals foraged in the crowns of the trees up to the tallest treetops (8–30 m) while calling frequently (LNS). They usually associated with other small tyrannids, such as Sclater's Tyrannulet

(*Phyllomyias sclateri*) and Slaty-capped Flycatcher (*Leptopogon superciliaris*), and various tanagers. These are the first records of *P. ophthalmicus* for Dpto. Santa Cruz, the southernmost ever for the species, and represent the white-bellied subspecies *P. o. ottonis,* which occurs north to northern Dept. of Puno, Peru (Traylor 1979).

Carmiol's Tanager (*Chlorothraupis carmioli frenata*).—Two groups of 4–8 of these tanagers were noted in dense undergrowth of forest along the Río Saguayo at 600–700 m. These are the southernmost records for the species, previously known only as far south as Dpto. Cochabamba (Isler and Isler 1987). Central American populations of the species are separated from South American populations (*C. c. frenata*) by 700 km, leading Ridgely and Tudor (1989) to suggest *C. c. frenata* be given species status. *C. c. frenata* itself is made up of several apparently widely disjunct populations found along the eastern Andes from Colombia south, but appropriate intermediate habitats may not have been adequately sampled.

As a final note to this paper, we wish to point out that although these forests on the eastern edge of the Andes are rich in additional endemic flora and fauna, not a single area north or south of Amboró National Park receives protection in Bolivia. Because of the biological and watershed value of these forests, we urge that support be given to the efforts of conservationists who seek to strengthen legal protection for Amboró and other Andean forests.

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T. A. PARKER, III, *Conservation International, Washington, D.C. and Museum of Natural Science, Louisiana State Univ., Baton Rouge, Louisiana 70803;* JOHN M. BATES, *Museum of Natural Science and Dept. of Zoology and Physiology, 119 Foster Hall, Louisiana State Univ., Baton Rouge, Louisiana 70803;* AND GUY COX, *% Fundación Amigos de la Naturaleza, Box 2241, Santa Cruz, Bolivia.* *Received 18 April 1991, accepted 1 Sept. 1991.*

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A hybrid Scissor-tailed Flycatcher × Western Kingbird specimen from southwestern Oklahoma.—At 18:30 CST on 11 May 1988, John B. Wheatley and Sam J. Orr noticed an unusual flycatcher 3.2 km south and 9.6 km east of Lawton, Comanche County, southwestern Oklahoma. The bird's tail was dark, deeply forked, and bordered with white but was shorter than that of a Scissor-tailed Flycatcher (*Tyrannus forficatus*), hereafter STF. Furthermore, its belly color was not white washed with salmon, but dull yellowish, similar to that of a Western Kingbird (*T. verticalis*), hereafter WK. Its flight displays and its call notes (recorded by Wheatley) resembled those of the STF.

The surrounding countryside was mostly open pastureland with a scattering of American elms (*Ulmus americanus*), hackberries (*Celtis occidentalis*), and mulberry (*Morus* sp.) trees. Both STF and WK were present in the area.

The bird was seen again on 12 and 13 May and photographed by Wheatley and Orr (photos not suitable for reproduction). On 16 May, Wheatley and Tyler found the bird again. Tyler collected it and prepared it as a museum skin (originally Cameron Univ. Museum of Zoology 1034, now Carnegie Museum of Natural History 168365). It proved to be a male, with the cranium incompletely pneumatized (flycatchers frequently exhibit delayed pneumatization). The right testis measured 6.5 × 13 mm, and the left testis was bilobed and strongly asymmetric. The weight was 43.3 g.

Color and pattern comparisons.—UNDERPARTS: The throat of the WK is gray, only slightly paler than the gray of the breast. That of the STF is pure white. That of the hybrid is nearly white, hence more like the STF.

In the hybrid, the transition between the pale neutral gray (86; numbered colors from Smithe 1975, 1981) of the breast and the trogon yellow (153) of the belly, washed with pale orange yellow (18) (richer on the flanks), is at about the same level as the gray to sulfur yellow (157) transition in the WK. The salmon-pink wash on the underparts of the STF begins more posteriorly. The crissum of the STF is near white, faintly flesh color (5). That of the WK is a dilute version of the sulfur yellow (157) of the belly. In the hybrid the crissum is a dilute version of trogon yellow (153). The under wing coverts and distal axillars of the STF are flesh color (5), changing proximally to spectrum red (11), which continues to the sides of the breast to form a semi-concealed (when the wings are folded) patch. The under wing coverts of the WK are a darker version of sulphur yellow (57), intensifying proximally only slightly. In the hybrid the under wing coverts and distal axillars are whitish, faintly washed with warm buff (118) becoming spectrum orange (17) proximally, blending on the flanks with the yellow of the belly.

UPPERPARTS: The crown and nape of the STF are pale neutral gray (86), those of the WK light neutral gray (85). Those of the hybrid are midway between. The concealed crown patch in the STF is very small, involving only about 3–4 feathers, nearest flame scarlet (15) in color. That of the WK is much larger, between flame scarlet and chrome orange (16) in color. In the hybrid the patch is intermediate in size, Pratt's ruby (210) centrally, changing laterally to a color between spectrum orange (17) and orange yellow (18).

The nasal bristles of the STF are white, those of the WK black. Those of the hybrid are white with black tips. The ear coverts of the STF are, if anything, slightly whiter than the crown. They are darker gray than the crown in the WK, forming a vague, relatively inconspicuous ear-patch. In the hybrid, the ear coverts are almost imperceptibly darker than the crown, but the feathers have whitish shafts.

The back of the STF is gray, barely darker than the pale neutral gray of the crown and nape. In the somewhat variable WK, the back feathers are basally rather darker than olive yellow (52), broadly tipped with the light neutral gray of the crown and nape, giving an overall grayish green appearance. In the hybrid, the back feathers tend to be gray basally and mixed gray and olive yellow on most of the web, giving a somewhat grayer overall appearance than in the WK. The upper tail coverts are dull black in both species and the hybrid.

WINGS AND TAIL: The remiges and wing coverts of the WK are near hair brown (119A), subject to much fading with wear. Those of the STF are similar but more neutral (less brown, more blackish). The coverts of the hybrid are near those of the WK in color, but the remiges are more blackish, closer to the STF. The upper wing coverts of the WK do not have contrasting edgings, although the tertials are edged with dull grayish white. In unworn specimens of the STF, the coverts, and especially the tertials, are conspicuously edged with white (slightly grayish on the lesser coverts). The covert edgings of the hybrid are mostly worn away, but what remains is grayer than in the STF. The tertial edgings of the hybrid are paler than in the WK but not as white as in the STF.

The outer web of the outermost rectrix (R6) in the WK is white (tinged yellow basally in fresh-plumaged specimens) for its full length except for the terminal 5 mm or so, where the black of the inner web crosses over the shaft to the outer web. In the STF, both webs of the outermost rectrix are white (tinged salmon basally in fresh-plumaged specimens) for about 65–75% of their length, at which point the inner web develops progressively more black, in a long taper beginning along the shaft, and crossing over to the outer web 30–40 mm from the tip. In the hybrid, the outermost rectrix pattern is essentially that of the STF, but the

black begins to appear at about halfway from the base, the taper along the inner web is more abrupt, and the black crosses to the outer web about 20 mm from the tip. In addition, the white is almost imperceptibly tinged with yellow.

The pattern of the next-outermost rectrix (R5) in the STF is similar to that of R6, but the black begins closer to the base, at about midway along the feather's length. There is no white in the tail of the WK other than that on the outer web of R6. In the hybrid, R5 is white for about its basal third.

UNFEATHERED PARTS: The bill, legs, and claws of the freshly collected hybrid were jet black (89). In the dried specimen, these parts are similar in color to those of specimens of the WK. The bill (in life?) of the STF is described by Oberholser (1974) as "dark brown, lighter at base, particularly on mandible"; this description fits dried specimens as well. The iris color of the hybrid was not recorded.

Measurements.—Twelve relatively unworn spring males of each of the putative parent species in the Carnegie Museum of Natural History were measured. The measurements taken were flattened wing to the nearest 0.5 mm, tail (standard measurement) to the nearest 0.5 mm, length of bill from anterior point of nostril to the nearest 0.1 mm, width of bill at base to the nearest 0.1 mm, maximum width of the outermost rectrix to the nearest 1 mm, and difference in length between the longest (outermost) and shortest rectrix (=tail fork) to the nearest 1 mm. The separation between the two species in the last two measurements was so great that no statistical computations, not even the means, were made. Measurements presented by Ridgway (1907) indicated that the tarsal length of the two species is almost identical, so this rather awkward measurement was not attempted. The two species were statistically inseparable in both of the bill measurements, which are therefore not reproduced here.

Wing: STF, 119–131 (124.75), SD 3.506; WK, 127–135 (130.5), SD 2.440; hybrid, 127.5.

Tail: STF, 189–241 (216.33), SD 17.369; WK, 90–100.5 (93.67), SD 2.783; hybrid, 130.

Maximum width rectrix 6: STF, 9–11; WK, 16–18; hybrid, 12.

Tail fork: STF, 140–166; WK, 2–5; hybrid, 46.

The hybrid is clearly intermediate in all measurements in which the two parent species differ. Its wing measurement is almost midway between the means of the two series.

Other structural characters.—In the STF, the outermost primary, P10 (only) is narrow and notched; the notch is 21–23 mm from the tip of the feather, and is attenuated distad to the notch (2–2.5 mm wide). In the WK, the *four* outermost primaries are progressively more attenuated at the tip, inner to outer, but as a smooth curve with no notch. The hybrid resembles the STF but without a distinct notch where the outermost primary narrows.

In the STF, the 2nd outermost primary (P9) is the longest, with primaries 7–1 progressively shorter. In the WK primaries 8 and 7 are equal and longest, with P9 barely shorter. In the hybrid, primaries 9 and 8 are equal and longest, with P7 barely shorter, and P10 (outermost) slightly shorter than P7.

Discussion.—In addition to the WK, two superficially similar species of *Tyrannus* are sympatric with the STF. One of these, Cassin's Kingbird (*T. vociferans*), is known to breed in Oklahoma only in Cimarron, westernmost county of the panhandle, roughly 500 km NW of the collection site of the hybrid (Sutton 1967). The area of sympatry of the STF and Couch's Kingbird (*T. couchii*) lies far south of Oklahoma. Nevertheless, as one referee pointed out, it is possible that the hybrid was not hatched in the vicinity of its collection site, so some consideration must be given to the remote possibility that one of these two kingbirds rather than the WK was a parent of the hybrid.

The bill of *T. couchii* is massively larger than that of either the WK or the STF, and has a more prominently keeled culmen. The breast is yellow, only slightly greener than the belly, rather than gray. There is no indication of intermediacy in either of these characters in the hybrid. The bill of *T. vociferans* is only slightly longer than that of the WK, but is distinctly

broader at the base. As emphasized above, the bills of the WK, STF, and the hybrid are essentially alike in size and shape. In addition, the gray of the head and anterior underparts of *T. vociferans* is much darker than in the WK; if this species had been a parent of the hybrid, one would expect this heavy pigmentation to be reflected to some degree in the hybrid, which it is not.

In virtually all color and structural characters, the Lawton, Oklahoma, specimen is midway between the STF and the WK, although in a few instances closer to one than the other. We are confident that the specimen has been correctly identified as a hybrid between *T. forficatus* and *T. verticalis*; the likelihood of a kingbird parent other than *verticalis* is considered to be virtually nil. Hybridization in the family Tyrannidae has seldom been reported (Short and Burleigh 1965), and we know of no other specimens of the parentage reported here (or between any other pair of *Tyrannus* species), but a sight record (with sonograms) of such a hybrid encountered in Austin, Texas, from 18 April to 22 June 1967 was reported by Davis and Webster (1970). Their color description suggests that the Texas hybrid more nearly resembled *T. forficatus* than does the Oklahoma bird, as its back was described as pale gray. Measurements taken from photographs of the Texas bird indicated that the tail and wing length were approximately equal, and this is also true of the Oklahoma hybrid. In *T. verticalis* the mean tail length is about 72% of the mean wing length; this proportion in *T. forficatus* is about 173%.

The Texas hybrid was paired with a female Western Kingbird. Davis and Webster stated that "The existence of the hybrid and its mating with *T. verticalis* demonstrate the phylogenetic proximity of *M[uscivora] forficata* and *T. verticalis,*" and they supported the suggestion of Smith (1966) that *Muscivora forficata* be placed in the genus *Tyrannus.* The American Ornithologists' Union (1983) subsequently placed both species of *Muscivora* in *Tyrannus.*

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Jack D. Tyler, *Dept. Biological Science, Cameron Univ., 2800 West Gore, Lawton, Oklahoma 73505-6377;* and Kenneth C. Parkes, *Carnegie Museum of Natural History, 4400 Forbes Ave., Pittsburgh, Pennsylvania 15213.* *Received 3 June 1991, accepted 3 Sept. 1991.*

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Natal dispersal and inbreeding in the Cooper's Hawk.—Dispersal data are important in understanding population ecology (Greenwood 1980, Shields 1984), but dispersal has been little studied in raptors (Belthoff and Ritchison 1989). Our 11-year study of breeding Cooper's Hawks (*Accipiter cooperii*) in Wisconsin has yielded data on natal dispersal (movement between birth place and breeding site [Greenwood 1980]) of six males and one female. We also report a grandson-grandmother mating involving one of these males. Records of inbreeding in natural populations of birds are rare, and this apparently is only the fifth record of close inbreeding in raptors (VanCamp and Henny 1975, James et al. 1987, Postupalsky 1989, Millsap and Bear 1990). We are unaware of other published data on natal dispersal and inbreeding in the Cooper's Hawk or its North American congeners.

These data are from birds marked as nestlings with U.S. Fish and Wildlife Service leg bands and, with two exceptions noted below, later trapped as breeding birds at their nests. Most of our data come from a population nesting in Waukesha County, southeastern Wisconsin (42°53′N, 88°29′W), as described in Rosenfield (1990). A "nesting area" is defined as that relatively small area (ca 800 m in diameter) within which a mated pair nests and conducts most other breeding activities in one or more years (Rosenfield 1990). A nesting area may or may not be reoccupied by the same or different adults in subsequent years (Rosenfield and Bielefeldt, unpubl. data). A "successful" nesting is one in which young reach bandable age (ca 14 days).

The fresh carcasses of males M1 and M6 (Table 1) were found on 14 July and 5 May, respectively. The nesting season for Cooper's Hawks in Wisconsin extends from mid-March into early August, and we thus assume that M1 and M6 (both at four years of age) were on or near their nesting areas when found (cf Newton 1986:256).

Males dispersed in all directions and moved an average of 12.0 km (Table 1). The female moved farther (14.4 km) than five of the six males. Although few, these data suggest that natal dispersal distances are probably greater in females, as found for other birds (Greenwood 1980), including some raptors (Newton 1986, Steenhof et al. 1984).

Male M3, the son of M2, bred successfully with his grandmother (the mother of M2) for three consecutive years (1988–1990) on the same nesting area where M2 fledged. It is difficult to determine if inbreeding depression, as noted for other species (Greenwood et al. 1978), has resulted from this mating because we do not know the familial relationship of the female to her mates in previous years on this nesting area. Nonetheless, the grandmother's mean clutch size from 1984–1987 was 4.0 eggs (range = 2–5) with earlier mates, and 3.7 eggs (range = 3–4) in 1988–1990 when mated with her grandson. In 1989, two of the three unhatched eggs in a clutch of four were infertile. In our 1980–1990 studies, this is the sole instance in which only one egg hatched from 4–5 egg clutches (N = 132).

Assuming that mean age at first breeding in Cooper's Hawks is ≥ two years (pers. obs.), we had a maximum of 43 opportunities to detect sibling or parent-offspring inbreeding at nests at which both breeders were marked and parental nesting histories were known. As noted, we detected inbreeding in three instances (7%) involving the same grandmother-grandson pair. Data from this single inbred pair at the same nesting area could conceivably inflate the observed frequency of inbreeding, yet rates are similar for separate nesting areas with ≥ one opportunities (5%, N = 22) or ≥ two opportunities (9%, N = 11) to detect inbreeding.

Inbreeding, if rare, is not easily detected. Newton (1986), for example, found no cases of inbreeding in a 14-year study of the European Sparrowhawk (*A. nisus*). Moreover, most reports of inbreeding probably represent a minimal estimate of its true frequency because it is usually impossible to mark all closely related individuals. We thus deem our minimal

TABLE 1
NATAL DISPERSAL OF SEVEN COOPER'S HAWKS IN WISCONSIN

Individual[a]	Year fledged	Year(s) encountered	Distance (km) and direction moved[b]	Comments
M1	1982	1986	35.2 SW	Found dead
M2	1984	1985–1990	12.8 N	M3's father
M3	1986	1988–1990	12.8 S	M2's son
M4	1986	1989–1990	2.4 NE	
M5	1987	1990	4.8 NE	F1's mate
M6	1987	1991	4.0 W	Found dead
F1	1987	1990	14.4 SW	M5's mate

[a] M = male, F = female.
[b] From hatching site to nesting area.

estimate of 7% for Cooper's Hawks to be a relatively high incidence of inbreeding. Studies of similar scope have also detected inbreeding rates of 9% in Merlins (*Falco columbarius*) (James et al. 1987) and 13% in Burrowing Owls (*Speotyto cunicularia*) (Millsap and Bear 1990). This relatively facile detection of inbreeding in Cooper's Hawks and other species of raptors warrants further study of its incidence and consequences as well as the factors that might promote or inhibit inbreeding in birds of prey.

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Robert N. Rosenfield and John Bielefeldt, *College of Natural Resources, Univ. Wisconsin, Stevens Point, Wisconsin 54481; and Park Planning, Racine County Div. of Public Works, Sturtevant, Wisconsin 53177.* *Received 9 May 1991, accepted 20 Sept. 1991.*

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Adult Common Loon feeding behavior is related to food fed to chicks.—We observed adult Common Loons (*Gavia immer*) feeding their young from hatching through fledging to determine the food types fed to chicks and to relate changes in adult feeding behavior to changes in the food types fed to the young.

Study area and methods.—We studied loons on lakes 55–100 km north of Sudbury, Ontario, that varied from 5.3 to 15.7 ha in area. Summer lake pH ranged from 6.7 to 8.4. We observed loons from 50–400 m with a 20×–60× spotting scope. We studied five loon families on five lakes between 25 July and 14 September, 1983 (50 h) and recorded the parents' dive durations, their foraging success rates (proportion of dives after which they surfaced with food and fed the young), and when possible, the types of food fed to the young. Chick age was estimated by using nest dates and the size of the chicks.

We also observed adults foraging for themselves (lone adults) on five lakes between 13 June and 11 July, 1983 (10 h). Lone adults were either non-breeders or breeders from other lakes. These birds never brought food to the surface, so we could not measure their foraging success rates nor determine what they were eating. We simply recorded dive durations.

Feeding.—We saw parents feeding their chicks vegetation and fish, as well as small items that we could not identify. The amount of vegetation decreased significantly from 65% of the identifiable food items for 4–15 day-old chicks to 4% for 46–74 day-old chicks, while fish increased significantly from 35% to 96% ($\chi^2 = 42.7$, $P < 0.001$, N = 169). The percentage of feedings for which we could identify the food item increased significantly from 18% to 48% for the same age groups ($\chi^2 = 32.0$, $P < 0.001$, N = 878). Correspondingly, foraging success rates of parents decreased significantly from 70% to 27% ($\chi^2 = 86.6$, $P < 0.001$, N = 1482), while mean successful dive durations (dives after which a parent surfaced with food) increased significantly from 18.2 ± 11.3 sec to 36.9 ± 15.0 sec (t-test, $P < 0.005$, N = 369 dives).

Mean successful dive durations of parents feeding their young were shorter than mean unsuccessful dive durations (dives after which parents surfaced without food), regardless of chick age. Since we could not distinguish successful dives from unsuccessful dives for lone adults, the only way to compare dive durations of lone adults to those of parents feeding chicks was to combine successful and unsuccessful dives. The mean dive duration for lone adults (45.8 ± 18.1 sec) was only slightly, though significantly, longer than the mean combined dive duration for parents feeding the oldest chicks (42.4 ± 14.3 sec, t-test, $P < 0.03$, N = 467).

Discussion.—Parents changed their feeding behavior according to the food they were securing for the chicks. During the first 4–6 weeks, the parents made short dives and brought up small food items that were often too small to identify. Later the parents made longer dives, often bringing up fish that were large enough to identify. These relatively large fish were presumably more difficult to catch than the smaller food items, and it appeared that the foraging success rate decreased. During the prefledging period, the mean dive duration of parents feeding their young increased almost to the mean dive duration of lone adults, suggesting that the food fed to chicks approached the adult diet of fish.

Other studies on loons indicate the importance of vegetation and invertebrates during the early prefledging period, as well as to a shift to fish. Young Arctic Loon (*G. arctica*) and Pacific Loon (*G. pacifica*) chicks are fed a diet consisting mainly of aquatic insects (Lehtonen 1970, Bergman and Derksen 1977, Sjolander 1978), which shifts to a diet of mostly fish after 40 days (Lehtonen 1970). As Red-throated Loon (*G. stellata*) chicks become older, the parents feed them fewer but larger fish (Reimchen and Douglas 1984). Vegetation may be important for young Yellow-billed Loon (*G. adamsii*) chicks, comprising about 15% of the food items fed to chicks less than about 35 days old (Sjolander and Agren 1976). Observations on Common Loon chicks (Munro 1945, Parker 1988) and Pacific Loon chicks (Bergman and Derksen 1977) indicate that they can be raised on a diet that does not include fish, provided that invertebrates (aquatic insects, crustaceans, and gastropods) are sufficiently abundant. All this suggests that invertebrates may have accounted for a significant proportion of the unidentifiable food items in our study, particularly for young chicks.

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Robert Alvo, *Ministry of the Environment, Box 21, 2360 ch. Ste-Foy, Ste-Foy, Quebec G1V 4H2, Canada*; and Michael Berrill, *Watershed Ecosystems Program, Trent Univ., Peterborough, Ontario K9J 7B8, Canada.* *Received 30 Oct. 1990, accepted 7 Sept. 1991.*

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Movement of a nestling between American Crow nests.—Intraspecific brood parasitism by egg moving and egg laying has been reported for 79 avian species (Yom-Tov 1980, MacWhirter 1989). MacWhirter (1989) pointed out that this is a newly reported and little-understood phenomenon. We located no published accounts of transferring nestlings between nests, and we found documentation of only two corvid species, the Black-billed Magpie (*Pica pica*) and the Pinyon Jay (*Gymnorhinus cyanocephalus*), moving eggs (Trost and Webb 1986). We here report evidence of nestling movement by the American Crow (*Corvus brachyrhynchos*).

While conducting a study of American Crows in central Iowa, we visited 59 nests to collect biological information and to band young. One nest was located in an urban woodlot in Ames, Iowa, about 0.5 km west of Iowa State University campus. The nest was situated about 10 m high in an ash tree (*Fraxinus* sp.). When we first climbed to the nest on 1 May 1979, it contained three eggs. Two adults also were present. On 8 May 1979, we again visited the nest and found three young estimated to be five days old based on an aging technique using size, skin color, opening of the eyes, and plumage development (Good 1952). Again, two adults were present. We took blood samples from each nestling by heart puncture. One died from this procedure, and we removed it from the nest.

On 30 May 1979, we visited the nest a final time to take more blood samples and to band the young. At this time, three 4-week-old young were in the nest, and five adults were present. The immigrant nestling must have been placed in the nest either as an almost terminally incubated egg or as a nestling. Because the age difference among the three young appeared to be only one or two days, the latter is likely. It is possible, however, for size and developmental disparities of nestlings of different ages to be minimized by disproportionate feeding (Skutch 1976).

The likelihood that the third nestling could have been a recent fledgling from a nearby nest is not supported for several reasons. During our last visit, all three nestlings stayed in the nest. We never observed a recently fledged crow exhibiting the same relatively passive behavior when approached by humans. Gross (1964) and Good (1952) stated that four-week-old nestling crows may stand on the rim of the nest or even go to nearby branches of the nest tree. At five weeks, they are able to leave the nest and make their initial flight. However, if disturbed, they may flee from the nest before five weeks. Kilham (1989) reported crows from two nests fledging at 37 and 41 days old. Of 38 nests we visited when young were estimated to be ≥ four weeks old, 17 stayed in the nest, 13 left when approached, and eight had fledged already. The closest known crow nest to the one on which we are reporting was about 500 m away. None of the three nestlings was capable of flying this distance.

We also do not think that the three additional adult crows engaged in mobbing behaviors during our last visit to the nest were necessarily parents of the immigrant nestling. It is not unusual for neighboring crows to assist one another in anti-predator behavior. We experienced mobbing groups of up to 20 individuals during the nesting season.

Crows are physically capable of transporting young nestlings. Goodwin (1976) and Gross (1964) reported several incidents of crows carrying relatively large objects, including an ear of corn by their feet.

Social aspects of crows also may be important factors allowing or contributing to nestling movement between nests. Cooperative nesting and strong long-term pair bonds have been reported for American Crows (Schaefer 1983, Kilham 1989). Schaefer (1983) even documented a two-year-old crow nesting only 0.5 km from its birth nest. Individuals with close familial ties would be more likely to interact and to exchange nest items than would unrelated birds.

All previous reports of egg moving have concluded that the natural parent bird moved the egg into the nest of a foster-parent-to-be. In this case, we should not exclude the possibility of the foster parent actually taking a nestling from another nest. Crows are extremely gregarious and interact with one another in many ways, including cooperative feeding and nesting (Kilham 1989). Yom-Tov (1976) found that Carrion Crows (*C. corone*) did not distinguish strange chicks introduced into their nests containing nestlings. McGowan (1990) reported an incident of Fish Crows (*C. ossifragus*) adopting a young Blue Jay (*Cyanocitta cristata*) that had gained access to the crow nest by unknown means.

Brown (1984) and Trost and Webb (1986) reported that synchronous nesting of Cliff Swallows (*Hirundo pyrrhonota*) and Black-billed Magpies may have facilitated intraspecific

nest parasitism. The average hatching date for central Iowa crows in 1979 was 1 May (N = 26; range = 25 April to 13 June). Nine of these nests hatched eggs during the first week of May. We consider this pattern asynchronous.

The frequency of nestling movement in crows appears to be low compared to other quantitative studies of intraspecific nest parasitism. Evidence of nestling moving was observed in only one (3%) of 31 nests we visited more than once. Brown (1984) reported that up to 24% of nests in various Cliff Swallow colonies were parasitized by colony members laying eggs in a conspecific's nest. Of 39 Black-billed Magpie nests examined daily, 38% had one to three eggs disappear between laying and the final day of hatching (Trost and Webb 1986). Three nests (8%) also had an unmarked egg appear toward the end of incubation.

Although we found no other report of nestling moving in the literature, its occurrence would be difficult to detect. Large avian nestling predators observed carrying unidentified nestlings probably are assumed to be transporting food items.

Because of its rarity, egg and nestling movements in crows and other species are difficult to study systematically and experimentally. Field biologists must be made aware of these reproductive strategies and be prepared to record incidental sightings.

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Joseph M. Schaefer and James J. Dinsmore, *Dept. of Animal Ecology, Iowa State Univ., Ames, Iowa 50011.* (Present address JMS: *Dept. Wildlife and Range Sciences, 118 Newins-Ziegler Hall, Univ. of Florida, Gainesville, Florida 32611-0304.*) *Received 16 May 1991, accepted 10 Aug. 1991.*

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Snowfall causes lek movement in the Sharp-tailed Grouse.—The Sharp-tailed Grouse (*Tympanachus phasianellus*) exhibits what has been termed "classical" lekking behavior. Males of classical lekking species occupy the same territory on the lek within and between years (Hohn 1953, Hamerstrom and Hamerstrom 1955, Koivisto 1965, Evans 1969). Although there are minor variations in boundary locations, the territories on leks are quite stable, which suggests that suitable landmarks must exist to provide cues for the lekking males (Evans 1969). This paper reports on the movement of Sharp-tailed Grouse leks within and between days due to unusual environmental circumstances.

The study sites consisted of areas of muskeg located in the James Bay region of northern Ontario, Canada. All observations were made during the morning "dancing" period. On 31 March 1990, a nucleus of nine birds arrived and began "dancing." Males that arrived later occupied territories peripheral to those of the individuals that arrived earlier. In this way, the late-arriving males made the early-arriving birds "central." At the end of the morning display period, there were twenty-two males displaying on this lek. On 1 April 1990, the lek formed in a similar fashion to that seen the previous day; however, the center of the lek had moved approximately 30.5 m from the position noted a day earlier. The area of muskeg that was the central region of the lek the day before was now flooded by water and was no longer suitable for "dancing."

Between 27–29 March 1991, a storm deposited 0.3–0.9 m of snow on the James Bay muskeg. On 30 March 1991, a nucleus of four birds arrived and began displaying. Eight other males arrived and established territories on the periphery of the original nucleus of birds. The lek was disturbed twice with the group members fleeing and then returning to establish the lek in a manner similar to that described above. That is, a nucleus of four birds arrived first and the late-arriving birds formed peripheral territories around these "central" males. However, although the lek was established in a similar fashion, three times in one morning, the position of the lek was in a different location each time.

The observations made on the two leks as described above suggest that stability of territories on leks can be affected by unusual environmental circumstances. In one case, flooding caused the lek to move 30.5 m from its location noted the previous day, and in the other, a snowstorm covered existing landmarks on the muskeg with the lek forming and reforming in three different locations in the same morning. Although the location of the lek changed in these two cases, the actual infrastructure of the lek appeared unchanged. In other words, individuals in the lek maintained their positions relative to one another. It is assumed that the nucleus of individuals that first started displaying were the same between mornings in 1990 and within the morning period in 1991. This assumption appears valid since the process whereby the infrastructure of the lek is established by central males that arrive first with peripheral individuals arriving later has been documented for other lekking grouse (e.g., Wiley 1973, Hartzler 1974). The above observations are suggestive that habitat landmarks may not be the only important cue used in maintaining the stability of territories in a "classical" lek; individuals may use their neighbors as "landmarks" on which to orient themselves.

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Leonard J. S. Tsuji, *Dept. of Biology, York Univ., North York, Ontario M3J 1P3, Canada.*
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Colonial nesting of the Orange Oriole.—The Orange Oriole (*Icterus auratus*) is endemic to the Yucatán Peninsula, México, but, despite being fairly common, little is known of its breeding biology. Only one set of eggs is reported in North American collections (Kiff and Hough, 1985. Inventory of Bird Egg Collections in North America, 1985. A.O.U. and Oklahoma Biol. Survey, Norman, Oklahoma) and the nest has not previously been described. Since 1974, de Montes has found numerous Orange Oriole nests in the states of Yucatán and Quintana Roo. Field observations indicate that the nest is a neat pouch constructed of plant fibers, varying in color from blackish to straw, depending on the predominant materials used. In general appearance it resembles the nest of Hooded Oriole (*I. cucullatus*) but tends to be slightly deeper. While visiting the Western Foundation of Vertebrate Zoology (WFVZ) recently, Webb found an uncatalogued, but labeled, Orange Oriole nest from "Yucatan," which allows a fuller description to be provided. The WFVZ nest is approximately 12.5 cm deep by 7.5 cm in diameter. It is woven of fine blackish plant fibers and in places is so thin that light passes readily through the walls. Typically *I. auratus* nests are slung between slender branches, often near the top of a tree or bush, at heights of 1–10 m above the ground. They thus tend to be conspicuous, in contrast to *I. cucullatus* nests which, in the Yucatán Peninsula, are slung under large leaves such as those of palms. Most Orange Oriole nests have been near or over water, e.g., around cenotes (natural limestone sinkholes) or in low flooded areas. Prior to 1988, de Montes had occasionally found two to three nests in close association.

On 4 July 1988, we located two Orange Oriole colonies in Si'an Kaan Biosphere Reserve, Quintana Roo. At the Caseta Chumpón entrance, we found 30–35 nests in an area of 80 × 30 m, with up to five nests in a single small tree. Nests were placed 2.5–9 m up in bushes and low trees in flooded scrubby woodland. Breeding was not synchronous, as some adults were still building nests, some were sitting in completed nests, others were feeding nest-bound young, and at least one stub-tailed juvenile was out of the nest, begging for food. Associated with the colony were two pairs of Hooded Orioles, a pair of nest-building Black-cowled Orioles (*I. dominicensis*), and at least three pairs of Black Catbirds (*Melanoptila glabrirostris*) that were feeding nestlings.

At Km 16.0 along the Chumpón access road, we located a colony of 26–30 pairs of Orange Orioles in an area of 60 × 25 m. Nests were placed 1–3 m up in flooded low scrub. All of the nests appeared to be completed and most, if not all, contained sitting adults. No other nesting species appeared to be associated with this second colony.

Although several species of Icterines are colonial nesters (Orians, "Blackbirds of the Americas," Univ. Wash. Press, Seattle, Washington, 1985), the phenomenon appears to be rare among the New World orioles, *Icterus*). Orchard Orioles (*I. spurius*) have been reported nesting in a colony (Dennis, in Bent, A. C., "Life Histories of North American Blackbirds, Orioles, Tanagers, and Allies," Dover Publications Inc., New York, New York 1958), but we have found no reference to other species of *Icterus* nesting colonially.

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Steve N. G. Howell, Sophie Webb, *Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970;* and Barbara M. de Montes, *Apdo. Postal 8, Cancún, Quintana Roo, México.* *Received 3 May 1991, accepted 4 Sept. 1991.*

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First observations of chick carrying behavior by the Buff-crested Bustard.—Parental transportation of young is known to occur in several taxa. Some waterfowl passively carry offspring by allowing chicks to ride on their backs (Johnsgard and Kear 1968). More exceptional are those species that deliberately pick up their young and carry them by means of grasping the chick with the claws, the bill, or the wing (Cobcroft 1934, Johnsgard and Kear 1968). Clapper (*Rallus longirostris*) and Virginia rails (*R. limicola*), gallinules (*Gallinula* spp.), sandpipers (*Actitus* spp.), both genera of woodcock (*Scolopax* spp. and *Philohela* spp.) and cuckoos (*Centropus* spp.) all carry chicks in this manner (Pettingill 1938, Welty 1982). The African Jacana (*Actophilornis africana*) and the Lotus-bird (*Irediparra gallinacea*) hold offspring under their wings while conveying them across lily pads (Hopcraft 1968, Cobcroft 1934). They accomplish this by gripping one or two chicks between the wing and the torso with the chicks' feet and legs dangling below the wing. Chick carrying has not been reported previously for the Buff-crested Bustard (*Eupodotis ruficrista*) although it is known in a few members of Otididae. The East Africa Natural History Society Nest Record Scheme contains a record made by J. F. Reynolds of a Hartlaub's Bustard (*E. hartlaubi*) carrying a three-day-old chick in Nairobi National Park. The Houbara Bustard (*Chlamydotis undulata*) (P. Gaucher, pers. comm.) and the Great Indian Bustard (*Choriotis nigriceps*) (Hasan 1982) are reputed to transport chicks clasped under the wing. This paper describes what are believed to be the first observations of this behavior in the Buff-crested Bustard.

A female Buff-crested Bustard at the Dallas Zoo has been observed carrying chicks (Fig. 1) during three consecutive breeding seasons. The first observation of this behavior occurred in July 1989. For the first few days after hatching, the single chick exhibited a lack of coordination due to poorly developed motor and visual faculties, characteristic of the species previously noted in hand-reared offspring. During this period, the female carried the chick under her wing on four observed occasions. Bouts were initiated when the hen was alarmed by human intrusion while brooding the chick under the wing. The hen stood while continuing to hold the chick gripped between the wing and the torso. The only visual indication of the chick's presence was its feet hanging below the hen's wing. After the hen moved away, the chick was dropped straight down, usually into the concealment of grass. During one observation of this behavior, the female remained standing motionless for approximately 30 sec, then relaxed and dropped the chick in its original location. At other times, she moved distances varying up to twelve feet (the distance limit of the enclosure) before dropping the chick in a new site. Two more observations of this behavior were made in July of 1990

FIG. 1. Female *E. ruficrista* carrying a chick. The chick's feet are visible extending below the female's left wing.

when this female reared another chick. Again, each bout of carrying occurred when the female was startled while brooding. In July of 1991, several more bouts of chick carrying were observed when this female reared a third chick.

The observed bouts of parental transportation of young in the Buff-crested Bustard appeared to be deliberate attempts to relocate offspring. My observations of Spur-winged Lapwings (*Vanellus spinosa*), which are also wing brooders, have shown that, when the hen stands abruptly, the chicks immediately drop out, often landing on their sides or heads. In contrast, bustard chicks drop straight down, normally landing in an upright position. It is possible that chick-carrying behavior is a defense mechanism that reduces predation of young by moving offspring to safety. A female, alarmed while brooding, gets up and moves away while the chick remains held under the wing. When dropped into the grass, the chick may go unnoticed due to its cryptic coloration. The need for the parent to remove its offspring from potential danger may be due to the chick's poor vision and clumsiness during the first few days after hatching. Since the behavior was observed only during the first three or four days after hatching, it is possible that as the chick's coordination increases, it becomes less necessary for the hen to intervene; the chick is able to hide itself. Another explanation is that the chick's growth causes cessation of this behavior when it becomes too large for the hen to carry. This is substantiated by observations of chicks falling out from under the wing at later ages. Further research is needed to conclude if this behavior is an idiosyncrasy of an individual or a species characteristic. Occurrence of chick-carrying behavior in two or three members of Otididae may suggest a previously unknown familial characteristic.

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and L. Fitzgerald for reviewing the manuscript. I am also grateful to the keepers in the Dallas Zoo Bird Dept. who made observations of this unusual behavior.

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CELIA K. FALZONE, *Dallas Zoo, 621 E. Clarendon Drive, Dallas, Texas 75203.* *Received 20 May 1991, accepted 5 Sept. 1991.*

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Long-eared Owl ingests nestlings' feces.—Female Barn Owls (*Tyto alba*) consume feces excreted by their small nestlings (Bunn et al. 1982:128). Hosking and Newberry (1945) watched a female Short-eared Owl (*Asio flammeus*) ingest dried nestlings' feces from about its nest. Indirect evidence of such behavior has been reported for Great Gray Owls (*Strix nebulosa*) (Nero 1980:118). Also, female Snowy Owls (*Nyctea scandiaca*) in semi-natural breeding chambers often consume the fresh feces of their small nestlings (K. McKeever, pers. comm.). I am unaware of published reports of similar behavior in other strigiforms.

On 16 June 1987, I observed an adult (presumably female) Long-eared Owl (*Asio otus*) at its nest in Burke County, North Dakota, from a blind 7 m away. Two of four 4–9 day old nestlings were fed by the adult at 09:40–09:50 CDT. Twice during this time, nestlings excreted feces onto the nest rim. Both times the adult immediately picked up and swallowed the feces. The feces appeared sac-like, similar to the mucous-covered fecal sacs of passerines and of small nestling Snowy Owls in breeding chambers (K. McKeever, pers. comm.). Nesting Long-eared Owls exhibit many predator-avoidance strategies (e.g., Bent 1938, Marks 1986). Removal of feces by ingestion could make nest sites less obvious to predators (Blair and Tucker 1941), although this hypothesis remains untested. Also, adult birds may ingest nestlings' feces to maintain nest hygiene or to obtain nutrients (e.g., Morton 1979).

Acknowledgments.—I thank M. Funk for field assistance and J. Marks for encouraging me to report this observation. The manuscript was improved by comments from R. Rosenfield, A. Sergeant, R. Eng, T. Gutzke, D. Holt, and P. Pietz, and benefited from communications with J. Marks, K. McKeever, E. Forsman, C. S. Houston, J. Marshall, C. Marti, D. Muir, and R. Nero.

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Robert K. Murphy, *U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, R. R. 1, Box 96C, Jamestown, North Dakota 58401 (address for reprints). Present address: Lostwood National Wildlife Refuge, R. R. 2, Kenmare, North Dakota 58746.* *Received 24 June 1991, accepted 11 Sept. 1991.*

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ORNITHOLOGICAL LITERATURE

SEABIRDS OF THE FARALLON ISLANDS: ECOLOGY, DYNAMICS, AND STRUCTURE OF AN UPWELLING-SYSTEM COMMUNITY. By David G. Ainley and Robert J. Boekelheide. Stanford University Press, Stanford, California 94305. 1900: xiv + 450 pp., 70 figs. 112 tables, 35 black-and-white photographs, appendices. $60.00.—In 1936, R. C. Murphy published the monumental "Oceanic Birds of South America," which, in addition to detailing the biology of southern hemisphere pelagics, was the first serious attempt to understand seabirds in light of their marine environment. Ainley and Boekelheide's study of the Farallon Islands seabirds extends that approach to a local ecosystem, with impressive results.

The Farallon Islands, 35 km west of San Francisco, are home to the largest and most diverse seabird assemblage in the continental United States, including two species of storm-petrels, one gull, three cormorants, and five alcids. In studies covering approximately 15 years (1971–1985), Ainley, Boekelheide, and their collaborators gathered an astonishing amount of detailed information on the biology, ecology, feeding habits, and reproductive success of the entire breeding avifauna, including species (e.g., Brandt's Cormorant, Ashy Storm-Petrel) for which basic biological data were scanty. These data provided the basis for carrying out their major goal, namely to understand how variations in the marine environment affect population dynamics and food resources. I have read few monographs that have succeeded so well in carrying out the authors' intentions.

The book starts with a general introduction to the area and the methods used. It continues with two major chapters. One documents the physical characteristics of the area, especially the zone of rich upwelling, and the ecology and abundance of the major prey species. The second is a masterful discussion of the feeding ecology of the avifauna and potential interspecific interactions; it even considers a summer visitor, the Sooty Shearwater, whose abundance may dwarf that of the breeding species. Following are chapters on the biology of individual species and, finally, a synopsis of "Patterns at the community level." Of the 12 chapters, Ainley wrote or contributed to 11 and Boekelheide eight.

The data are unparalleled and confirm—should any doubt remain—that long term studies are not a luxury. They are essential for showing that environmental conditions are far from static, even over a short time, and that changes in species assemblages are incessant. The dynamics of change are best illustrated by studies that luckily coincided with the most intense El Niño of our time. This disrupted the abundance of prey and caused the birds to switch diets and foraging areas. As a result, it had quite different effects on the productivity and recovery periods of each of the breeding species.

This book presents a wealth of information on seabirds, but its importance extends far beyond the marine environment. For example, Ainley presents cogent arguments that seabirds usually face their greatest challenges in winter, not during the breeding season; this supports a growing body of evidence (mostly generated from arctic waterfowl) that the condition of an individual at the end of winter is a major determinant of its subsequent reproductive success. He also argues that, at least on the Farallons, the size of breeding populations is more strongly affected by competition for nesting space (sometimes with marine mammals) than by competition for food. Another major and surprising finding is that, despite the abundance of food in this rich upwelling system, the breeding success of most species is largely dependent an the abundance of a single prey, juvenile rockfish (*Sebastes* spp.).

The authors' intelligent use of statistics contributes greatly to the usefulness of this volume. As a result, the reader is not distracted constantly by parenthetical tests of significance, but can follow the authors' reasoning and appreciate the kinds of data that made statistical tests necessary.

I found this book to be full of challenging ideas—some still to be tested. It will be read profitably by anyone interested in population dynamics, life histories, and long term studies. I have used it to compare population data from other areas, to see whether the trends noted at the Farallons might be recognizable on a broader scale. And it should be required reading for those who would presume to "manage" ecosystems in some mythical steady state.

In sum, this is a splendid book that has significance far beyond the little rocky islets that provided the data. I congratulate the authors and Point Reyes Bird Observatory for the tremendous effort needed to carry out this project, and I eagerly await a 10-year update.—J. R. Jehl, Jr.

Appalachian Spring. By Marcia Bonta. Univ. of Pittsburgh Press, Pittsburgh, Pennsylvania, 1991: xiv + 187 pp., 2 maps, small decorative drawings, $19.95 (cloth), $9.95 (paper).—This modest book is a first-class addition to the genre of naturalist diaries. Marcia Bonta is a freelance editor and writer who has lived for 20 years on a 500-acre mountaintop farm in central Pennsylvania. The exact locality of the farm is nowhere given; an arrow on one of the maps indicates that Tyrone is an unspecified distance to the north. Mrs. Bonta's observations of birds, mammals, lower vertebrates, insects, and plants are both knowledgeable and perceptive. After an introductory "Prelude" chapter summarizing winter, the diary begins on March 1 and ends on June 21. There is an index, lacking in many such books of essays, and a five-page bibliography that includes both books and selected journal articles.

It is hard to imagine that there would be anything controversial in a work of this type. However, on pp. 131–133, she describes having watched a black rat snake (*Elaphe obsoleta*) preying on starling nestlings. She then comments: "Although I may not be as fond of the snake family as I am of birds, for me to interfere on the side of the birds would have been an arrogant decision that presumes my wisdom is greater than nature's . . . I am content to believe that the web of nature is too intricate for me to meddle with, even on so small a scale as destroying a black rat snake to protect young birds." In *Bird Watcher's Digest* 13 (6), 1991, pp. 93–96, Mrs. Bonta relates a similar episode involving rat snake predation on a brood of House Wrens, including a vivid description of the snake's tenacity and ingenuity in working its way to an all but unreachable nest. She then discusses at somewhat greater length her family's philosophy of "not favoring one wild creature over another." This article resulted in an outpouring of letters to the editor, Mary Bowers; as of 25 July 1991, only 3 favored the Bontas' position, the rest varying from calm and intelligent letters suggesting that the snake should have been removed but not killed to others that were downright violent (M. Bowers, pers. comm.). A sampling of these letters (1 pro Bonta, 4 con) appeared in the next issue of *Bird Watcher's Digest,* with a list of other protesters and an editorial statement to the effect that a future article will address readers' concerns and feelings about this subject. I am tempted to make an editorial comment of my own about this emotional approach to natural predation, but will leave that instead to the calm and diplomatic wording of Mrs. Bowers and Mrs. Bonta.—Kenneth C. Parkes.

Four Neotropical Rainforests. Edited by Alwyn H. Gentry. Yale Univ. Press, New Haven, Connecticut. 1991. 627 pp., 97 numbered text figs., 108 tables. $57.50.—This multiauthored volume attempts an overview of the floristics, birds, mammals, reptiles and amphibians, and forest dynamics of two Central American and two South American forests, all four of which are well known to Neotropical researchers. The four forests are the La Selva Biological Station in Costa Rica, Barro Colorado Island and Pipeline Road in Panama,

Cocha Cashu Biological Station in Peru, and the Minimum Critical Size of Ecosystems Project near Manaus, Brazil. The book is divided into six parts: the sites, floristics, birds, mammals, reptiles and amphibians, and forest dynamics. Obviously the five chapters on birds will be of most interest to readers of *The Wilson Bulletin,* so this review will focus on those chapters.

The total volume numbers 627 pages including indexes, of which 108 are devoted to birds. This includes an 18 page appendix which is a combined list of all species seen at the four sites along with other summary information (habitat preference, mass, ecological classification) on each species. The chapters are brief and much of the information in each bird chapter is based on mist-netting data.

The chapter on La Selva, Costa Rica is authored by John G. Blake, F. Gary Stiles, and Bette A. Loiselle. A total of 410 bird species have been recorded at La Selva, of which 256 breed. The area consists of primary forest, forest edges and gaps, rivers and streams, scrub, anthropogenic second growth, old plantations, and pastures. Seventy percent of the breeding bird species are in some way directly associated with forest, and 55% of the non-breeding species are forest associated. Data indicate that resident birds use forest interior more extensively than gaps. Migrants, both latitudinal (from North America) and altitudinal, comprise about 30% of the avifauna. Altitudinal migrants utilize forest interior heavily while latitudinal migrants are mostly associated with non-forest and forest edge habitats. Mist-netting held no surprises. The most successful nets were in young and second growth areas, probably due at least in part to sampling realities. Low canopy areas have better capture rates than high canopy areas. Migrants from the temperate zone were most frequently captured in young second growth, and least captured in interior forest. The authors conclude that "maintenance of second growth areas at La Selva will probably be necessary to ensure continued existence of a variety of species."

The chapter on Barro Colorado Island (BCI) and Pipeline Road in Panama is authored by James R. Karr. Karr notes that BCI is a recently isolated land bridge created during the construction of the Panama Canal, and thus the avifauna has changed over the past 70 years, since BCI was isolated. A total of 444 bird species have been recorded from BCI and nearby Pipeline Road (on the mainland), of which 370 species are regular in occurrence, and 278 breed. Regarding habitat affiliation, 55 species are tied to lakes and rivers, 64 are associated with open second growth areas, and 251 are forest species, but "forest" includes old second growth, interior streams, canopy, edges, and gaps. A total of 66 species have become extinct from BCI, largely due to loss of early successional habitat as the forest has returned. Karr summarizes his extensive mist-netting studies including species accumulation curves, relative abundances, trophic structure, capture rates, and survival rates.

The chapter on Cocha Cashu Biological Station in the Peruvian Amazon is authored by Scott K. Robinson and John Terborgh. This area, located in southeastern Peru, includes Manu National Park, and is considered a possible regional center of avian endemism, with 550 total bird species of which 435 are resident. Habitats are varied, including oxbows, floodplains, beaches, cane thickets, high ground forest, open forests of bamboo, upland forest, and lake margins. Data were obtained from mist netting (including some canopy nets) and song censuses. Charles Munn mist netted 45 species in canopy nets 30–50 m above ground, of which 22 had never been captured in ground level nets inside mature forest. Song censuses revealed that many forest species have large territories (between 5–50 ha) but most species in early successional areas have small territories (approx. 0.25 ha). Species distribution is generally patchy and, in spite of very high species richness, rarity is common. High richness multispecies flocks are characteristic of the forest.

The chapter on the Minimal Critical Size of Ecosystems (MCSE) project, located 80 km north of Manaus, Brazil, is authored by Richard O. Bierregaard, Jr. The data presented are

confined to mist netting of the understory bird community. The forest is located on ancient nutrient-poor soils and the study areas are on three 15,000 ha cattle ranches, comprising a mosaic of pasture, second growth, isolated forest fragments, and virgin forest. A total of 352 species were seen of which 143 were netted. Ninety percent of the netted species were considered to be numerically rare. Mixed species insectivorous flocks predominated but there were also obligate ant followers among the most frequently netted species. The only North American migrants netted were Veery (*Catharus fuscescens*) and Gray-cheeked Thrush (*C. minimus*).

Following the four chapters on birds is a brief summary chapter by Karr, Robinson, Blake, and Bierregaard. The differences among the four sites are not insignificant. North American migrants were much more represented in the two Central American sites. The Amazonian sites demonstrated the importance of habitat diversity (many species are affiliated with specific habitat types), and the prevalence of high richness but general rarity of individual species. The authors present an impressive summary but note accurately that our general knowledge of Neotropical birds still remains "rudimentary."

I recommend this book to anyone seriously interested in Neotropical ecology. Each chapter is well-referenced, citing other studies from that particular area. The editing is sound and the book is free of typos and other annoying errors. One strong criticism, however, is that only in the chapter by Bierregaard do common names of bird species appear. The other bird chapters use only scientific names, which is no longer necessary since common names of Neotropical bird species are well standardized. Many, if not most readers of *The Wilson Bulletin* will need to have the relevant field guides or some other volume at hand to understand which species are being discussed.

I also wish to note that the other chapters dealing with floristics, forest ecology, mammals, and reptiles and amphibians are insightful to anyone with a general interest in the Neotropics.—John C. Kricher.

Écologie et Comportement des Gobe-Mouches (Aves: Muscicapinae, Platysteirinae, Monarchinae) du Nord-est du Gabon. Volume 2: Organisation sociale et Écologie de la Reproduction des Muscicapinae. By Christian Érard. Mémoires du Muséum National d'Histoire Naturelle, Série A, Zoologie, Tome 146, Editions du Muséum, Paris. 1990:233 pp., 101 figs., 15 tables, ISBN 2-85653-178-4. 320 FF or 125 Dutch Guilders (available, plus 10% postage, from Universal Book Services, Dr. W. Backhuys, Warmonderweg 80, 2341 KZ Oegstgeest, The Netherlands).—In the first volume of this work (which I reviewed in Wilson Bull. 101:669–760, 1989), Érard discussed the community structure of 30 Old World flycatcher species living in rainforests of northeastern Gabon. In this volume, Érard analyzes in detail the 13 species of Muscicapinae occurring in his study area. He approaches the problem of how this restricted community is organized by "examining this time the eco-ethological characteristics that are particular to each species, in order to better define the relationships between the community [*peuplement* in French] and its environment" (p. 19). Further, Érard explains that he introduces "the ethological dimension in the structure of the community at the same time as [he] analyzes, with a population-level and a species-level emphasis, the organizational systems that each species has adopted, in response to its fundamental biological requirements, to best utilize the resources of the environment" (p. 19).

The data presented in Volume 2 were gathered, as were those in the first volume, during Érard's eight trips to northeastern Gabon for a total of 25 months of work in rainforest; over 5000 hours were devoted to observations of flycatchers in the field. This sample size is very impressive.

In the first part of the book (Socio-ecological characteristics of the species belonging to the Muscicapinae community, pp. 23–193), Érard describes for each species (*Muscicapa striata, M. cassini, M. sethsmithi, M. epulata, M. olivascens, M. caerulescens, Myioparus griseigularis, M. plumbeus, Pedilorhynchus comitatus, Artomyias fuliginosa, Stizorhina fraseri, Fraseria ocreata,* and *F. cinerascens*), social units, territorial systems, vocalizations, breeding biology, and molt. For five of these species (*Muscicapa striata, M. cassini, M. sethsmithi, Fraseria ocreata,* and *F. cinerascens*) he also discusses breeding productivity and mortality. The depth of treatment varies from species to species, from 3 pages for *Myioparus plumbeus* to 20 pages or more for five species (*Muscicapa cassini, M. sethsmithi, Stizorhina fraseri, Fraseria ocreata,* and *F. cinerascens*). Apart from *Muscicapa striata,* a Palearctic species that does not breed in his study area or, indeed, in the Afro-tropical Region, the twelve other species studied by Érard breed in northeastern Gabon. For each of these twelve species, the information available in the literature prior to Érard's work was scattered and largely anecdotal. Thus, these treatments represent a giant step forward in our understanding of the fundamental eco-ethological characteristics of these species. Furthermore, since Érard studied these species as members of a functional biological community, the accounts are comparative and highly informative. Each account is richly illustrated with diagrams, tables, sonagraphs, and photographs, documenting aspects of their biology such as displays, vocalizations, nest sites, and data on breeding seasonality.

In the second part of the book, entitled "Discussion" (pp. 195–221), Érard focuses his attention on three main themes: (1) socio-ecological patterns based on taxonomic comparisons, (2) socio-ecological patterns based on habitat comparisons, and (3) patterns based on comparisons of social systems. In spite of the wealth of data, Érard, in the present work as well as in his previous monograph, is very cautious about how to interpret this information. He reminds the reader that "the data [he] gathered were, for the most part, the first information available on the biology of these species" (p. 219) and that "it is also the first time that a community of tropical birds is analyzed in such a detailed manner," so that the lack of comparative information from other similar communities and the lack of uniformity in amount of data across species place severe constraints on the generality of his conclusions. I commend Érard for his prudence, but I must warn the reader who might take Érard's caution too seriously that, in my opinion at least, few, if any, data sets on any comparable tropical avian community exist, hence that the observations and conclusions reported by Érard in the two volumes of this series represent a set of baseline studies against which all others will be measured.

On the whole, it seems that north-temperate Muscicapinae differ from their tropical counterparts in Gabon in several important respects. Tropical taxa are more diverse morphologically and eco-ethologically, are more complex in their social behavior, and are K-strategists. The spatio-temporal environmental mosaic provided by the Gabonese rainforest (including biological factors as well as random, catastrophic-type events), is a very important source of background heterogeneity that modulates or is tracked by the various facets of diversity of the birds themselves, thus producing a rich array of responses in terms of adaptive strategies. Whereas interspecific competition plays a clear role in this tropical flycatcher community, the exact roles of predation remain to be fully worked out, although predatory pressures are important. A puzzle is why these flycatcher species should be territorial, when in fact their low population density would at first sight seem not to be conducive to their having evolved territorial systems. What set of resources, then, act as the limiting factors that allow territorial behavior?

Once again, I congratulate Érard for an extremely thorough and stimulating piece of work on Afro-tropical birds. Once more, I urge him to publish some of his work in English, so

that his unique data set and insights into tropical forest ecology and behavior become as widely known as they deserve. In the meantime, I urge all tropical avian ecologists, ethologists, and evolutionists to acquire Érard's monographs and to study them.—François Vuilleumier.

Wings for my Flight. By Marcy Cottrell Houle. Addison-Wesley Publishing Co., Inc., New York, New York. 1991: 187 pp., $17.95.—Marcy Cottrell Houle's narrative account of observing a nesting pair of Peregrine Falcons (*Falco peregrinus anatum*) at Chimney Rock, Colorado in 1975 not only gives us insight into the behavior of these magnificant birds of prey but also portrays a realistic and not always so pleasant or romantic view of a field biologist's working conditions. Just out of college and working for the state of Colorado, Ms. Houle and her partner, Ms. Alex Porter of the U.S. Forest Service, were caught in the conflict between those who wanted to develop this ancient Anasazi Indian site for tourism and the few who felt the falcons should be left relatively undisturbed during the nesting season. The fact that they were young and women in a traditionally male role added to the difficulties in dealing with some members of the community.

Aside from the excessive anthropomorphic interpretations of the falcon's behavior, we get an in depth description of the peregrine's activities in different stages of development from the time of incubation until the two young could hunt for themselves, approximately four months. The blend of biology and ecology, with a touch of history of the Anasazi Indian site where the falcons chose to nest, make for enjoyable and easy reading.

Ms. Houle's perseverance and dedication to the protection of the Peregrine Falcon is admirable and an incentive not only to young biologists just getting started but to those of us who get a little more than discouraged with the struggle to protect endangered species and their habitats. *Wings for my Flight* should be suggested reading for science students from age 16 on.—Donna Mitchell.

Bird Trapping and Bird Banding. By Hans Bub (Translated by Frances Hamerstrom and Karin Wuertz-Schaefer). Cornell University Press, Ithaca, N.Y. 330 pp, 456 black and white photos and diagrams. $69.50.—Have you ever thought of building a Helgoland trap for banding purposes? Or is the Bal Chatri the solution to your raptor banding project? Is a research program being held up by your inability to capture and color mark the study species? Or are you just curious about the many ways the human mind has devised to capture live birds, whether for research purposes or as in some societies, to add to the evening's menu? All of these questions might have answers in this book, which is a English translation of a book originally published in Germany in 1978. We owe a debt to Fran Hamerstrom and her co-translator for translating this useful compendium of bird capture techniques.

Bub has combed the international literature going back as far as the Sixteenth Century for discussions of bird trapping. It is difficult to imagine that there are methods of trapping not discussed in this book. Some of the methods included are: small or medium funnel traps, large funnel traps, cage traps, pit traps, stationary nets, bow nets, clap nets, pull nets, and cannon nets. There are specialized chapters on capturing ducks and other waterbirds, on the use of nooses, catching by hand, and catching at night. All these methods are profusely illustrated with drawings of traps, diagrams of netting sets etc.

Directions are given for the construction of most of these trapping devices. These include proper knots on a Bal Chatri, the proper way to erect a line of mist nets, and devices for

triggering clap nets. Full directions are given for the operation of large scale netting projects such as cannon nets.

A long chapter discusses the use of lure birds to entice new birds into the traps. As is pointed out in a forward by George Jonkel, formerly Chief of the U.S. Bird Banding Laboratory, this practice is illegal in the United States and Canada.

American bird banders faced with unusual problems will certainly profit from this book and the newcomer to banding whose experience does not go beyond mist netting will find much of interest and instruction.—George A. Hall.

Wisconsin Birdlife. Population & Distribution Past & Present. By Samuel D. Robbins, Jr., Univ. of Wisconsin Press, Madison, Wisconsin. 1991:xvii + 702 pp, colored frontispiece by Owen Gromme, 54 halftones, 170 maps. $75.00.—After a long lull, the day of the sumptuous "state birdbook" apparently is back. The present volume is the third to appear in the last few years. Others are on the way. Wisconsin had had no full treatment of its birds since Kumlien and Hollister's 1903 publication until Owen Gromme, of the Milwaukee Public Museum, set out in 1939 to prepare a state book in the classical tradition. Gromme spent most of his time painting a set of plates for the book and in ferreting out specimens of the more unusual records of the past. By 1960 it was apparent that these plates might well be published alone, and in 1963 Gromme's "Birds of Wisconsin" appeared with a set of color plates, accompanied by simple range maps and brief statements about the status of each species. In 1969 the project for a more complete text was turned over to the present author, long one of the leading bird students of the state.

The data base that Robbins had to work with was enormous, and it is apparent that he has mastered it. The Wisconsin Society of Ornithology is a large and active group and has published detailed bird records for nearly 50 years. A bibliography of 25 pages of fine print and a long list of observers follow the text. Robbins made an effort to become personally familiar with all parts of the state, and he has lived in several different places.

Part 1, The Background, starts with a chapter on the development of Wisconsin Ornithology which traces the history of bird observations through the years, and concludes with summaries of work done by the W.S.O. and the state agencies in recent years. One gets the impression that not much was done between the pioneering efforts of men like Kumlien, Hoy, and others until the 1940s when the W.S.O. was founded, although a list of 41 ornithologists active from 1850 to 1940 is given. Names such Leopold, Stoddard, and Schorger on this list are known beyond the borders of Wisconsin.

The second chapter is a unique discussion of the ecology of the state. While Wisconsin lacks dramatic changes in topography, it does present an interesting and complicated ecological picture. The southern forest region meets the northern forest region along a "tension zone" which stretches diagonally across the state from northwest to southeast. Interspersed in both regions are areas of transition to the prairie formation. In a 56-page chapter, The Landscape and the Birds, a perceptive and articulate ecologist, James Hall Zimmerman, discusses this complexity. This is the best description of ecological background that I have seen in a state bird book.

Zimmerman makes a return in the final part of the book with a long discussion of habitat preferences, which includes a table of breeding species showing the occurrence of these species into 29 habitat types. A less detailed table does the same thing for wintering species. This is a unique feature in a state bird book.

Robbins recognizes 394 species confirmed for the state, with 13 additional hypothetical species. Thirty-three of these have been added to the list since 1960. Is this a biologically significant indication of dispersal trends, or is it an indication of increased birding activity and increased sophistication of the birders?

The species accounts, which constitute the bulk of the book, occupy a little more than one page each. Besides a table briefly outlining status, and a range map, the accounts follow no set formula. Rather they are readable discussions of whatever Robbins found interesting about the distribution of the species or the timing of its migration. As is usual in state lists the author finds it hard to avoid giving more detail about the unusual species than about the common ones. There is little mention of population numbers except for the use of Breeding Bird Survey (BBS) data for the species who breed throughout the state. These data from 1966–1980 are averaged within the eight avifaunal zones recognized by the author.

The range maps usually include only those records made since 1960 and vary in quality. For widespread species the BBS averages are given. For species whose breeding range, or wintering range embraces only part of the state the ranges are indicated diagrammatically and other records are also included. The inclusive ranges seem to be stippled in approximately rather than accurately plotted. In some cases they disagree slightly from those plotted by Temple (1987, Wisconsin Birds. A Seasonal and Geographic Guide). One notes that a suite of boreal species all essentially have the same range.

My only serious criticism of the book is that the reader gets the impression that bird distributions and populations are constant. Little attention to changes in range over the 150 years is given. There is no good information about the avifauna of northern Wisconsin in the 19th century, but the southern half of the state was reasonably well known then so that historical comparisons could have been made. For a few species such as the Northern Cardinal (*Cardinalis cardinalis*) which have made dramatic invasions of the whole state within the memory of living people, there is a map showing the dates of arrival county by county.

Other than a rather perfunctory listing in the introductory chapter of species thought to be declining, there is little mention that bird populations are changeable. The averaging of the BBS data obscures any trends that might have occurred in the 16 years covered. Since current interpretations of the BBS data consider that most declines have occurred since 1980 this may not be as serious as it seems.

Since Gromme's earlier book had featured colored paintings of all species there are no bird pictures in this book, except an excellent painting of Pileated Woodpeckers (*Dryocopus pileatus*) by Gromme which serves as a frontispiece and also graces the dust jacket. The only other illustrations are photographs of some of the important ornithologists of the past.

The book was written with three groups in mind: (1) serious-minded amateurs, (2) professional ornithologists, and (3) the growing number of people interested in birds in a more casual manner. There is something for all of these, and it is hoped that the book will have wide circulation throughout the state. There is little about Wisconsin birds that cannot be learned from it. In brief this is one of the very best state bird books and as a one time author of a state book I wish mine could have come close to matching it.—George A. Hall.

SHORT REVIEWS

Current Ornithology. Volume 8. Edited by Dennis M. Power. Plenum Press, New York, New York. 1991:xiv + 335 pp. $75.—The latest volume of this useful work follows the high standards set by the earlier issues. There are seven review papers: A Review of New Zealand Ornithology by Allan J. Baker; Avian Radioecology by I. Lehr Brisbin, Jr.; Facultative Manipulation of Sex Ratios in Birds: Rare or Rarely Observed by Patricia Adair Gowaty; Enemy Recognition and Response in Birds by Ian G. McClean and Gillian Rhodes; Parasites and Sexual Selection in New Guinea Avifauna by Stephen G. Pruett-Jones, Melinda A. Pruett-Jones and Hugh I. Jones; Deceit and Mating Status in Passerine Birds: An Evaluation of the Deception Hypothesis by Hans Temrin; and Age-Specific Foraging Proficiency in Birds by Joseph M. Wunderle, Jr.—G.A.H.

Atlas Des Oiseaux de France en Hiver. By Dosithée Yeatman-Berthelot. Société Ornithologique de France, (55, Rue de Buffon, 1500S) Paris. 1991:575 pp, many maps, black & white sketches. 650 francs.—After completing a breeding bird atlas in 1976, the French ornithologists under the late Laurent Yeatman applied the Atlas methodology to the wintering birds, and we now have this impressive publication as a result. The now-familar atlas grid maps show the winter distribution of 246 regular and 56 occasional species as determined in the years 1977–1981. Each account is accompanied by a page of comment and a small breeding season map if the species breeds in France.—G.A.H.

The Ohio Breeding Bird Atlas. By Bruce G. Peterjohn and Daniel L. Rice. The Ohio Department of Natural Resources, Columbus, Ohio. 1991:xiv + 416 pp., colored cover, many black & white photos and maps. $20.—The latest addition to the growing shelf of state breeding bird atlases is this handsome volume from the Buckeye state. The book follows the now well-known Atlas format. Each species occupies a double-page spread with a large grid map showing the distribution occupying one page. The opposite page gives a short discussion of the species and each species is shown a black-and-white photograph. Over 500 volunteers found evidence of 193 species breeding in the state (182 confirmed). An appendix lists 10 species which were sighted during the atlas project but apparently do not breed. Another appendix discusses the physiographic regions of the state and is illustrated with 16 habitat photographs.

Ohio is a state without dramatic habitat changes, but the student of avian distribution will note how many breeding ranges are delimited by the line of glaciation which extends diagonally across the state. One also notes the several isolated pockets that support some presumed "boreal" species.

This very successful atlas project supplies the detail of distribution that was one of the few gaps occurring in the senior author's recently published "The Birds of Ohio" (review in Wilson Bull., 103:157–159 (1991).—G.A.H.

Birds of the Smokies. By Fred J. Alsop III. Great Smoky Mountains Natural History Association, Route 2 Box 272B, Gatlinburg, Tennessee 37738. 1991:167 pp, 100 colored photographs. $9.95 (paper).—This attractive little publication discusses 100 common birds of the Great Smoky Mountains National Park. Each species is illustrated with an excellent colored photograph taken by the author. A few paragraphs of descriptive text and a diagram showing the seasonal distribution at different elevations accompanies the photograph. Also included is a complete check-list of the birds recorded in the Park, descriptions of a few good birding sites, and "The Birder's Dozen," suggestions as to where to find the 12 most sought after species. This is an excellent buy for the first-time park visitor.—G.A.H.

New Journal: Bird Conservation International. Published for I.C.B.P. by Cambridge University Press. Vol. 1 No. 1, March 1991. £25 (Inquiries for subscriptions to Cambridge University Press, 40 West 20th Street, New York, New York 10011).—This new quarterly journal will focus on major conservation issues facing birds, especially globally threatened species and their habitats. The first issue has articles on birds from Dominica, Madagascar, Guinea, and French Polynesia.—G.A.H.

Wilson Bull., 104(1), 1992, pp. 203–204

INFORMATION FOR AUTHORS

The Wilson Bulletin publishes significant research and review articles in the field of ornithology. Mss are accepted for review with the understanding that the same or similar work has not been and will not be published nor is presently submitted elsewhere, that all persons listed as authors have given their approval for submission of the ms, and that any person cited as a personal communication has approved such citation. All mss should be submitted directly to the Editor.

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Style and format.—The current issue of *The Wilson Bulletin* should be used as a guide for preparing your ms; all mss must be submitted in that format. For general matters of style authors should consult the "CBE Style Manual," 5th ed., Council of Biology Editors, Inc., Bethesda, MD, 1983. Do not use footnotes or more than two levels of subject subheadings. Except in rare circumstances, major papers should be preceded by an abstract, not to exceed 5% of the length of the ms. Abstracts should be informative rather than indicative, and should be capable of standing by themselves. Most units should be metric, and compound units should be in one-line form (i.e., $cm\text{-}sec^{-2}$). The continental system of dating (19 Jan. 1950) and the 24 hour clock (09:00, 22:00) should be used.

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Editor Charles R. Blem
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Virginia Commonwealth University
816 Park Avenue
Richmond, Virginia 23284-2012

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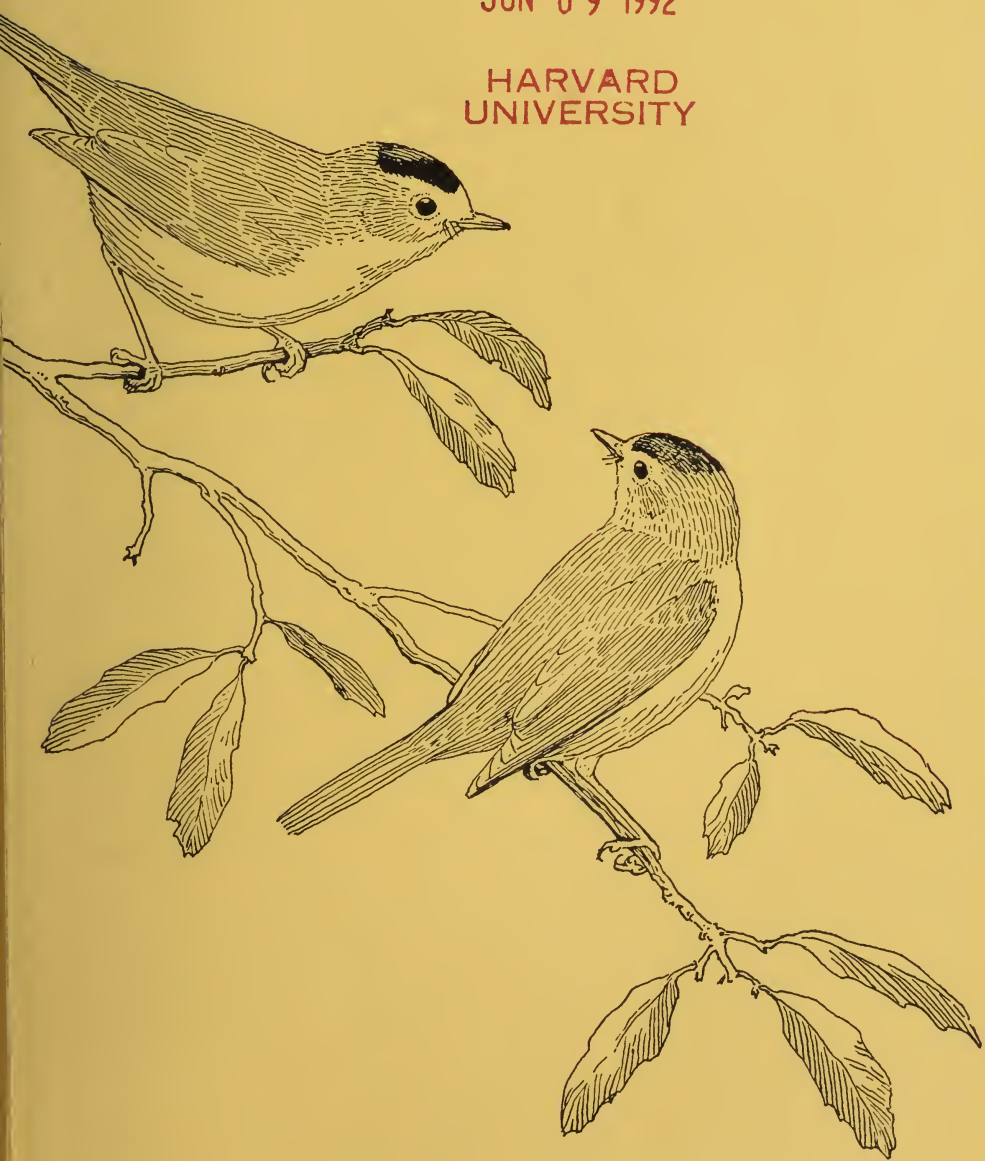

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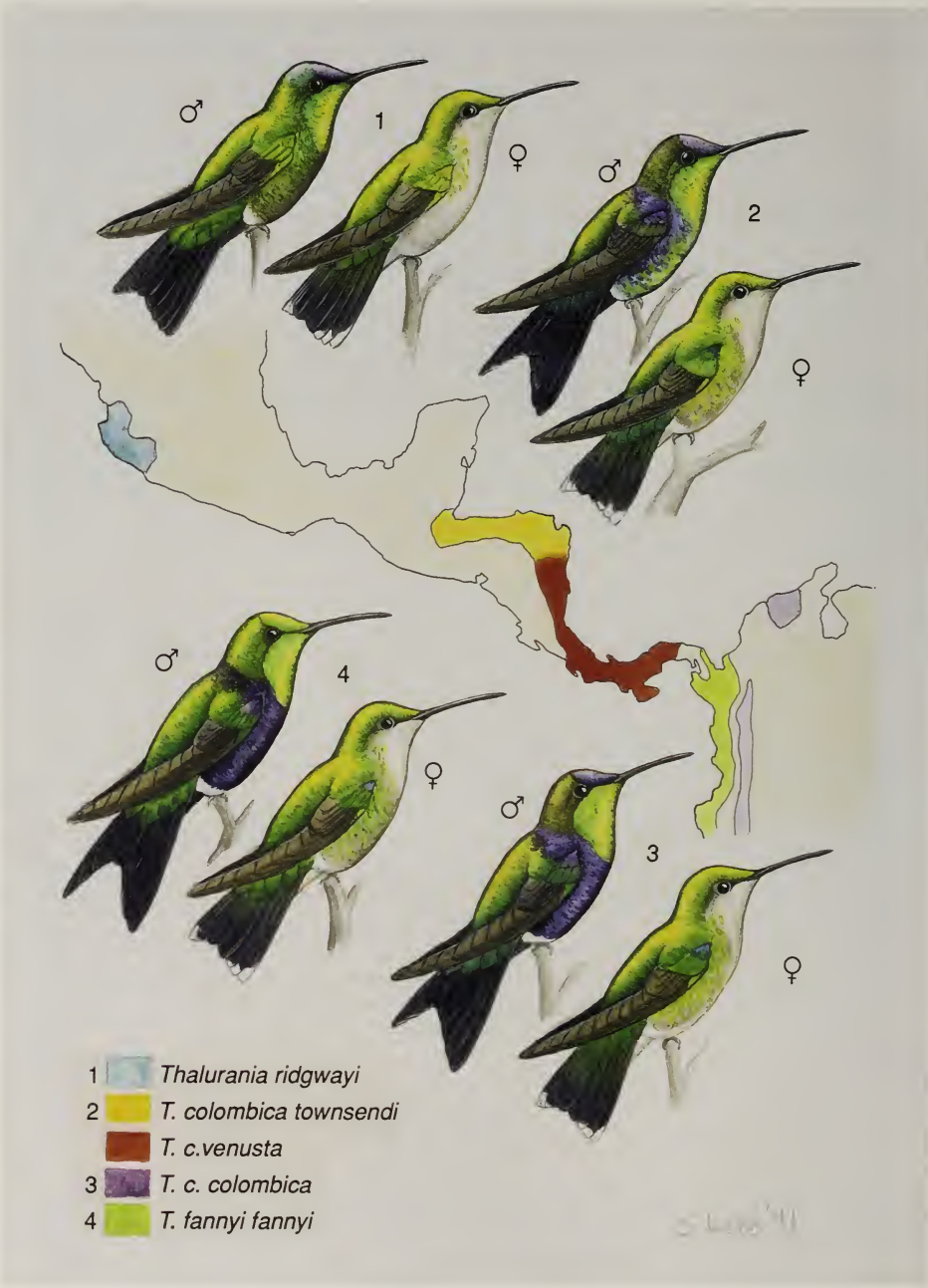

Middle American Woodnymphs. Painting by Sophie Webb.

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Wilson Bull., 104(2), 1992, pp. 205–219

GEOGRAPHIC VARIATION AND SPECIES LIMITS IN MIDDLE AMERICAN WOODNYMPHS (*THALURANIA*)

PATRICIA ESCALANTE-PLIEGO[1] AND A. TOWNSEND PETERSON[2]

ABSTRACT.—We analyzed geographic variation in morphology and plumage coloration in male woodnymphs of the genus *Thalurania* in Middle America and northwestern South America. Morphometric characters distinguish the disjunct western Mexican populations from populations to the south. Three groups are distinguished by discrete plumage coloration characters. We propose that these groups be recognized as separate species: *T. ridgwayi* of western Mexico; *T. colombica* of Central America south to western Panama and disjunctly in interior northwestern South America; and *T. fannyi* of eastern Panama, western Colombia, and northern Ecuador. *Received 11 July 1991, accepted 20 Sept. 1991.*

RESUMEN.—En este trabajo analizamos la variación geográfica en morfología y en patrones de coloración en el plumaje de los machos de las "ninfas de bosque" del género *Thalurania* de Mesoamérica y noroeste de Sudamérica. Los caracteres morfométricos distinguen las poblaciones del oeste de México de todas las poblaciones del sur. Con base en la coloración del plumaje, caracteres discretos separan tres grupos. Proponemos que estos grupos sean reconocidos como especies distintas: *T. ridgwayi* del oeste de México; *T. colombica* desde Centroamérica hacia el sur al oeste de Panamá y continuando después en el noroeste de Sudamérica; y *T. fannyi* del este de Panamá, oeste de Colombia y extremo norte del Ecuador.

In spite of more than a century of study, patterns of geographic variation and speciation in Middle American birds remain poorly understood. Studies employing modern, quantitative approaches are rare (e.g., Johnson 1980). The purpose of the present study is to analyze morphometric and plumage variation in Middle American populations of woodnymphs, hummingbirds of the genus *Thalurania*. Although of limited geographic

[1] Dept. of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192.
[2] Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, Louisiana 70803. Present address: Div. of Birds, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605.

FIG. 1. Geographic range of woodnymphs in Middle America and northwestern South America. Regions for statistical analysis are defined by solid lines; subspecies limits reflecting taxonomy of Peters (1945) are divided by thick lines.

scope (Middle America), we hope that this effort will stimulate other studies of the group as a whole.

As currently recognized, the polytypic Crowned Woodnymph (*T. colombica*) ranges in lowland tropical forest from eastern Guatemala south to northern South America (Fig. 1; A.O.U. 1983), where it is replaced by a congeneric allospecies, the Fork-tailed Woodnymph (*T. furcata*). Poorly known disjunct populations are found in humid canyons and foothills of western Mexico in the states of Nayarit, Jalisco, and Colima. Field surveys in suitable habitat in the intervening area of central and southern Mexico have not provided records of woodnymphs (e.g., Blake 1950, Binford 1989, Navarro et al., in press). Because woodnymphs are usually fairly common where present (Wetmore 1968, Stiles et al. 1989; pers. obs.), the gap between the ranges seems real and not simply a result of incomplete knowledge.

The western Mexican population of woodnymphs was described by Nelson (1900) as a distinct species (*T. ridgwayi*), based on a single male specimen. The form was known only from the type until the 1950s (Phillips 1961), and was eventually merged with the South American species (*T. furcata* by Peters [1945]) and maintained as a subspecies. The availability of new material from Nayarit (Escalante 1988) and Jalisco (recent

collections by the Field Museum of Natural History, the Laboratorio Natural Las Joyas de la Sierra de Manantlán, and others) prompted us to review the Middle American populations to document patterns of geographic variation and re-evaluate their taxonomic status.

The distribution of *Thalurania* in Mexico is somewhat unusual. Most Neotropical species ranging into the lowlands of western Mexico (e.g., Olivaceous Woodcreeper [*Sittasomus griseicapillus*], and Golden-crowned Warbler [*Basileuterus culicivorus*]) also are present in the east from Tamaulipas southward and have rather continuous ranges (Friedmann et al. 1957, Miller et al. 1957, Escalante et al., in press). However, several other western Mexican bird species show interrupted distributions similar to *Thalurania,* with closely related populations in Central America or northern South America (e.g., White-fronted Swift [*Cypseloides storeri* sp. nov.]-White-chinned Swift [*C. cryptus*] [Navarro et al., in press], Tufted Jay [*Cyanocorax dickeyi*]-White-tailed Jay [*C. mystacalis*], White-throated Jay [*Cyanolyca mirabilis*]-Silvery-throated Jay [*C. argentigula*], Red-breasted Chat [*Granatellus venustus*]-Rose-breasted Chat [*G. pelzeni*]; A.O.U. 1983).

Plumages of male woodnymphs vary dramatically among populations, forming a mosaic of forms characterized by different combinations of plumage characters that make the genus difficult to interpret taxonomically. Some taxonomists lump populations with glittering forecrowns (*colombica* group; Central America and northwestern South America) and those with dull-forecrowns (*furcata* group; interior South America) into one species (*T. furcata,* Peters 1945, Meyer de Schauensee 1970). Other authors recognize the various differentiated forms as constituting two or more species (e.g., Eisenmann 1955, A.O.U. 1983, Hilty and Brown 1986). The remaining two species in the genus, *T. glaucopis* and *T. watertonii* (as in the original description of Bourcier 1847 and not "*watertoni*" as Salvin 1892 or Cory 1918), of eastern Brazil also have glittering forecrowns. Other diagnostic characters of these two species, such as a green belly, deeply forked tail, and either a violet back (*watertonii*) or no violet on the back (*glaucopis*) are also present in Middle American woodnymphs, although not as pronounced. Clearly, a revision of the entire genus is in order; this paper, however, is restricted to Middle America and extreme northwestern South America, owing to the paucity of specimens and our own lack of experience in other critical areas.

METHODS

We examined a total of 171 specimens of adult male woodnymphs (Appendix I) in 12 museum collections: Academy of Natural Sciences of Philadelphia; American Museum of Natural History; Delaware Museum of Natural History; Field Museum of Natural History;

Instituto de Biología, Univ. Nacional Autónoma de México (UNAM); Los Angeles County Museum of Natural History; Louisiana State Univ. Museum of Natural Science; Museo de Zoología, Facultad de Ciencias, UNAM; Museum of Comparative Zoology; National Museum of Natural History; Peabody Museum of Natural History; and Univ. of California at Los Angeles. A common problem in studies of geographic variation is that females are underrepresented, as was true in the present case. However, variation in females appeared more or less parallel to that of males, although not accompanied by discrete differences in plumage characters in Middle American populations.

We recorded four measurements and three color characters from each study skin. The measurements were: BILL length from the anterior edge of the nostril to the tip, WING chord, TAIL length, and tail NOTCH (difference in length between the long outer rectrices and short central rectrices). Plumage characters included the following: percent of belly colored black, violet, or green; extent of the violet band on back (scored from 0 = absent to 3 = complete); and percent of forecrown violet vs green.

Because sample sizes at particular localities were small, we partitioned individual samples into ten regions (Fig. 1). Regions were established so that localities within each held more or less continuous habitat and so as to coincide with the distribution of named forms. Division among regions were somewhat arbitrary in northern Central America where habitat is continuous. To check the magnitude of geographic variation within regions, we compared measurements from three relatively large individual locality samples within region D (Appendix I).

To locate zones of significant morphological change, we conducted analyses of variance on each morphometric character, using Gabriel's test (sum of squares—simultaneous test procedure, SS-STP, Gabriel and Sokal 1969) on latitudinal sequences (Power 1970). We used two principal component analyses (PCA) to investigate multivariate patterns of variation among regions. First, we extracted principal components from the variance-covariance matrix of log-transformed regional means of measurements; the coefficients obtained were used to calculate individual scores and project them in multivariate space. This procedure projects variation on axes that maximize variance among regional samples (Gibson et al. 1984). A second PCA included two plumage characters (crown and belly), with the measurement data, and was based on the correlation matrix of untransformed regional means. Because within-sample distributions of back-band extent shows strong departures from normal distributions, this character is excluded from the multivariate analyses.

RESULTS

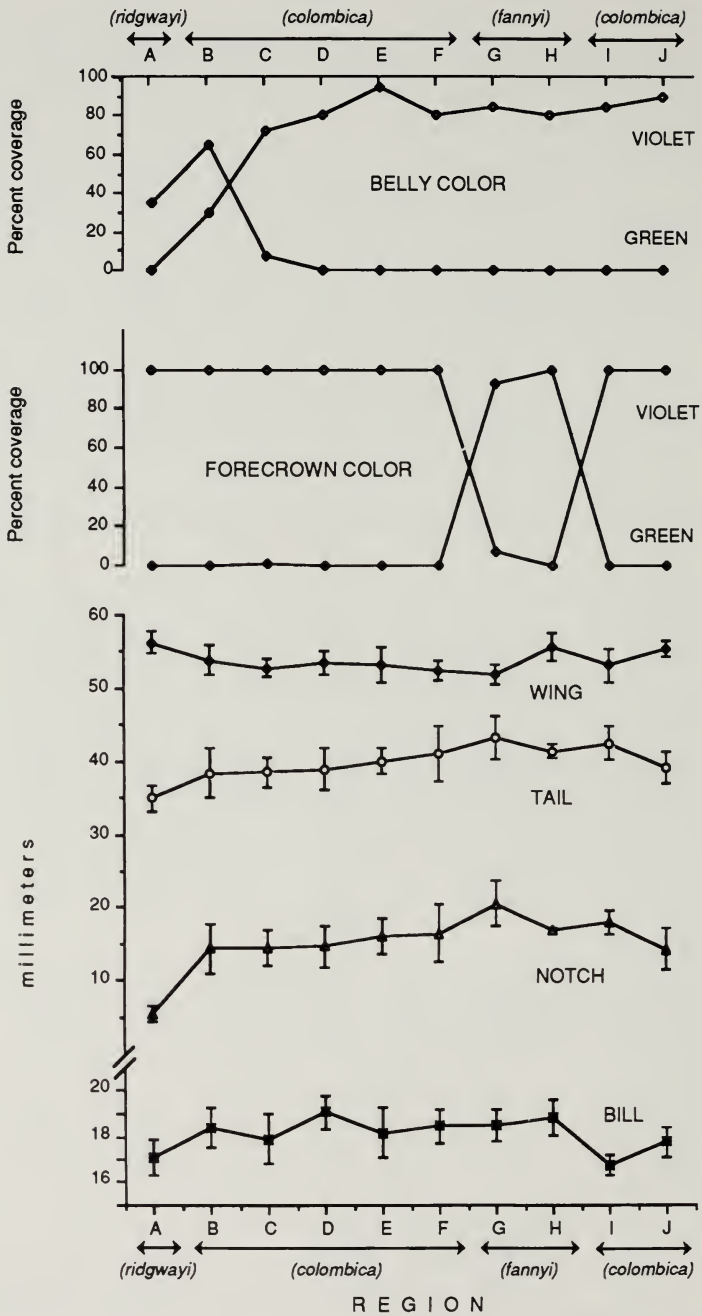
Plumage coloration.—Color patterns show striking differences between regions (Table 1, Fig. 2). Individuals of the western Mexican populations (region A) have predominantly green or black bellies; Guatemalan and Honduran populations (B) are intermediate in belly color, having both green and violet on the belly; Nicaraguan populations (C) have largely violet bellies but still retain some green. Populations farther south have completely violet bellies. Geographic patterns in the second color character, extent of the violet band on the back, are simpler: western Mexican populations have the back completely green with no band, but individuals of all remaining populations have either a complete band or two separate violet scapular patches.

A different geographic pattern is found in forecrown color (Fig. 2). The

TABLE 1

DESCRIPTIVE STATISTICS FOR COLOR PATTERN AND CONTINUOUS VARIABLES OF MIDDLE AMERICAN AND COLOMBIAN WOODNYMPHS. MEDIANS FOR COLOR CHARACTERS, AND MEAN AND STANDARD ERROR FOR MEASUREMENTS ARE PRESENTED. REGION LABELS FOLLOW FIG. 1.

	Region									
Character	A	B	C	D	E	F	G	H	I	J
N	19	32	18	26	13	15	19	5	8	15
Belly										
Violet %	0.0	30.0	72.5	80.0	95.0	80.0	85.0	80.0	85.0	90.0
Green %	35.0	65.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Black %	65.0	15.0	20.0	20.0	5.0	20.0	15.0	20.0	15.0	10.0
Back band										
Median	0.0	2.0	3.0	2.0	3.0	3.0	2.0	1.0	2.0	1.0
Forecrown										
Violet %	100.0	100.0	100.0	100.0	100.0	100.0	7.5	0.0	100.0	100.0
Green %	0.0	0.0	0.0	0.0	0.0	0.0	92.5	100.0	0.0	0.0
Bill										
Mean	17.11	18.39	17.91	19.06	18.16	18.45	18.49	18.82	16.74	17.75
SD	0.18	0.16	0.25	0.16	0.31	0.20	0.16	0.39	0.14	0.17
Wing										
Mean	56.27	53.87	52.78	53.44	53.25	52.34	51.87	55.67	53.10	55.37
SD	0.36	0.38	0.30	0.32	0.68	0.34	0.31	0.81	0.92	0.29
Tail										
Mean	34.92	38.29	38.42	38.90	40.03	40.96	43.23	41.38	42.42	39.04
SD	0.46	0.61	0.51	0.55	0.52	1.27	0.73	0.45	0.81	0.5
Notch										
Mean	5.41	14.33	14.40	14.55	15.93	16.40	20.45	16.78	17.84	14.18
SD	0.27	0.65	0.62	0.58	0.69	1.32	0.80	0.16	0.58	0.72


(ridgwayi)
(colombica)
(fannyi)
(colombica)
A
B
C
D
E
F
G
H
I
J
Percent coverage
100
80
60
40
20
0
VIOLET
BELLY COLOR
GREEN
Percent coverage
FORECROWN COLOR
VIOLET
GREEN
millimeters
60
50
40
30
20
10
WING
TAIL
NOTCH
20
18
16
BILL
REGION

six northernmost and two southernmost populations have violet forecrowns; two intermediate populations (the Darién region of Panama [G], and Choco, Columbia [H]), have green forecrowns. One to several violet feathers at the rear edge of the forecrown are observed in most Panamanian specimens (region G). The last color character, extent of forecrown, shows no detectable geographic differentiation.

Body dimensions.—Only three of 40 within-region character distributions depart significantly from normality, a level expected with a 5% significance criterion. TAIL and NOTCH are positively correlated (overall $r = 0.87$), but this correlation across samples varies greatly (e.g., region H, $r = 0.45$; region F, $r = 0.92$), indicating that both characters provide some independent information. Hence, all morphometric characters are retained for further analysis, and no transformations are employed except for multivariate analyses. Analyses of microgeographic variation among the three localities within region D indicate significant differences in three of the four characters (bill $P < 0.01$, notch $P < 0.04$, tail $P < 0.001$), suggesting the existence of microgeographic differentiation. However, the scale of these differences is considerably smaller than the among-region differences, so, owing to generally low sample sizes, we combine sites within regions.

SS-STP shows that western Mexican populations (A) differ significantly from southern populations in all dimensional characters and have a nonoverlapping distribution of NOTCH (Figs. 2 and 3). For the remaining regions (B to J), several patterns are evident. In BILL, regions B and C form a subset different from the remaining southern populations in which bill length increases gradually southward to region H and then decreases in I and J. In WING, southern populations show a gradual decrease in wing length south to Panama (region F) and then an increase in Colombian populations. In both TAIL and NOTCH, populations show a gradual increase from north to south, peaking in region G and decreasing in H–J.

Multivariate analyses.—For measurement data alone, the first principal component reflects mainly variation in NOTCH (Table 2). The western Mexican populations separate completely in multidimensional space along the first component (Fig. 4A). The rest of the populations overlap broadly, roughly arrayed in a north-to-south sequence. Specimens from eastern

←

FIG. 2. Geographic variation in belly and forecrown colors, and measurement data in male woodnymphs of Middle America and northwestern Colombia. *Y* error bars indicate standard deviations.

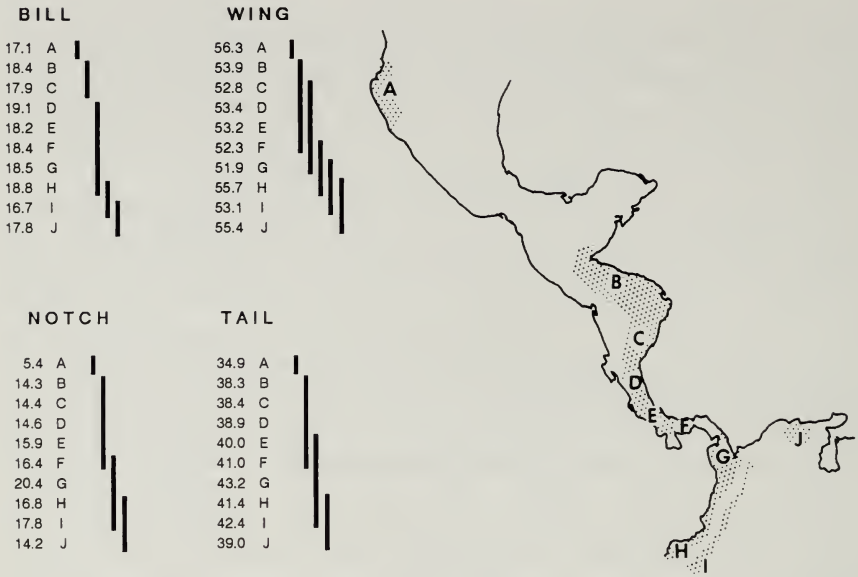


FIG. 3. SS-STP's of bill, wing, tail, and notch of populations of woodnymphs from Middle America and northwestern Colombia. Vertical bars indicate homogeneous subsets of populations.

Panama (region G) cluster tightly at the edge of the cloud but do not separate completely.

In the PCA of six measurements and plumage characters, a clearer pattern is found (Fig. 4B). The first and fourth principal components show the greatest separation between regions, together explaining 58% of the total variation (Table 2). Again, western Mexican populations separate along the first component, followed by a rough north-to-south sequence of the remaining populations. The eastern Panamanian (G) and Chocoan (H) populations separate on the fourth component.

DISCUSSION

The overall pattern of geographic variation in Middle American woodnymphs suggests the existence of three distinct groups. The disjunct western Mexican populations (*ridgwayi*) differ significantly in seven of eight characters, with a nonoverlapping distribution of NOTCH. The second group (*colombica*) is formed by the populations of Central America from Belize and Guatemala south to western Panama and continuing disjunctly in the upper Magdalena Valley (Huila) and Santa Marta region of Colom-

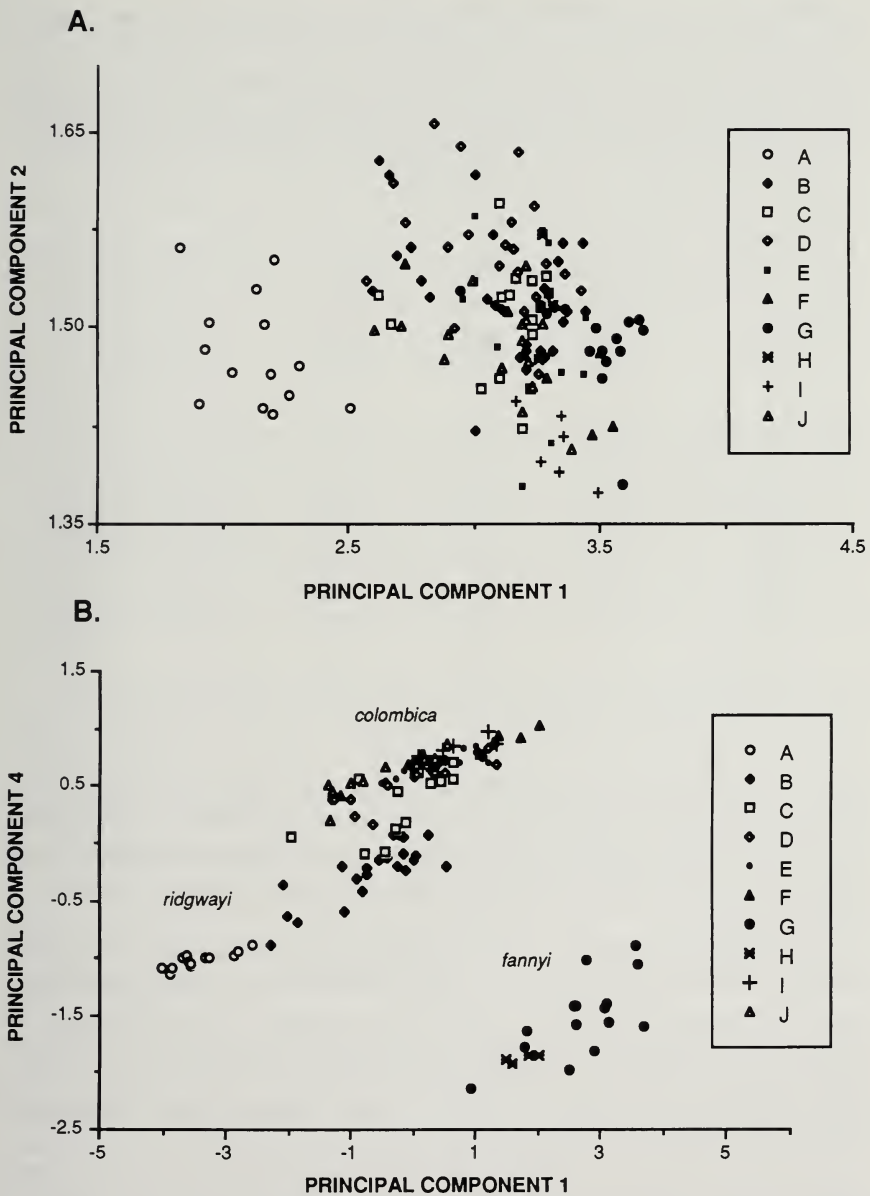


FIG. 4. Principal component scores based on (A) population means of morphometric characters, and (B) population means of morphometric and plumage characters of male woodnymphs of Middle America and northwestern Colombia. Labels correspond to regions in Fig. 1.

TABLE 2

PRINCIPAL COMPONENT COEFFICIENTS FOR (A) LOG-TRANSFORMED REGIONAL MEANS OF MEASUREMENTS, BASED ON THE VARIANCE-COVARIANCE MATRIX, AND (B) UNTRANSFORMED DATA, BASED ON THE CORRELATION MATRIX OF COLOR CHARACTERS AND MEASUREMENTS COMBINED FOR MALE WOODNYMPHS FROM MIDDLE AMERICA AND NORTHWESTERN COLOMBIA

	Character	Factor				
		PRIN1	PRIN2	PRIN3	PRIN4	PRIN5
(a)	Bill	0.045	0.925	0.315	−0.207	—
	Wing	−0.049	0.040	0.467	0.882	—
	Notch	0.986	0.018	−0.118	0.117	—
	Tail	0.152	−0.377	0.818	−0.407	—
	Eigenvalue	0.14	0.001	0.00	0.00	—
	Proportion	0.98	0.01	0.00	0.00	—
(b)	Belly	0.433	−0.202	−0.156	0.480	0.710
	Forecrown	−0.367	0.086	0.009	0.863	−0.335
	Bill	0.184	0.596	−0.770	−0.017	−0.111
	Wing	−0.282	0.712	0.402	−0.005	0.486
	Notch	0.559	0.139	0.202	0.139	−0.233
	Tail	0.501	0.264	0.424	0.066	−0.284
	Eigenvalue	2.72	1.02	0.91	0.76	0.49
	Proportion	0.45	0.17	0.15	0.13	0.08

bia. *T. colombica* shows pronounced geographic variation in belly color, changing gradually from green to violet on the belly between Guatemala and Costa Rica. The third group (*fannyi*) is formed by the eastern Panamanian, Caucan and Chocoan populations, based on differences in forecrown color.

Taxonomic implications.—A lively debate has centered around species concepts in ornithology (Cracraft 1983, McKitrick and Zink 1988); issues under discussion include the importance of gene flow, monophyly of species, and operational difficulties in applying species concepts. Although reproductive isolation has traditionally been used for defining species limits (biological species concept), we concur with Cracraft (1983) and McKitrick and Zink (1988) that the ability to reproduce is a shared ancestral trait that can be differentially retained, potentially confusing the reconstruction of the evolutionary histories of taxa. Furthermore, because of its dependence on the reproductive isolation criterion, the biological species concept is not directly applicable to allopatric taxa such as several of the forms treated in the present study.

The extreme application of the biological species concept to wood-

nymphs led to combining populations from Middle America to southern Brazil, Paraguay, and Bolivia into a single highly polytypic species, *T. furcata,* with 21 subspecies (Peters 1945). Differentiated allopatric forms and discrete segments of stepclines are treated as subspecies. Based on results presented above, for Middle American and northern South American woodnymphs, a putative biological species, *T. colombica,* could be recognized (including the five subspecies *ridgwayi, townsendi, venusta, fannyi,* and *colombica*) or a superspecies with three allopatric or parapatric species, the monotypic *ridgwayi* and the polytypic *fannyi* and *colombica.* The latter treatment, which separates the green-crowned *fannyi* populations, is supported by the fact that forecrown color is the character differing most dramatically in one of the few tests of sympatry in the genus (*T. furcata* and *T. glaucopis*).

Under the phylogenetic species concept, the three discrete sets of woodnymph populations in our study (*ridgwayi, colombica,* and *fannyi*) could be recognized as species. *T. ridgwayi* is differentiated in all measurements, is completely separable on the basis of NOTCH, and has no violet on the scapulars or back. Other diagnostic characteristics, such as the violet forecrown and green belly are perhaps primitive within the genus because potentially homologous character states occur in other members of the genus.

T. colombica is diagnosable only on the basis of a combination of violet back-band and forecrown, because both characters occur independently in other forms of the genus. If the presence of these characters in other taxa were confirmed as homologous, it would imply that perhaps *T. colombica* does not fit the monophyly requirement of the phylogenetic species concept. This question can be resolved only through a cladistic analysis of all members of this complex. Although further subdivision of *T. colombica* to the level of the described subspecies might be possible based on belly color, we prefer not to divide this form further because of the intermediate nature of most individuals in populations B and C in this character (Fig. 2).

The third lineage, *T. fannyi* is separable by its green forecrown. Although a green forecrown also occurs in *T. watertonii* and some forms of *T. furcata* of southcentral Brazil and Bolivia (*baeri*), it is neither as well defined nor as glittering as in *fannyi,* and so the glittering green forecrown in *T. fannyi* may represent a unique character.

A phylogenetic analysis based on biochemical characters is clearly necessary for resolution of these questions for the entire genus. In the meantime, we propose the following taxonomy for the northern representatives of *Thalurania,* based on criteria from biological and phylogenetic species concepts: (1) *Thalurania ridgwayi* Nelson, Ridgway's Woodnymph, west-

ern Mexico; (2) *Thalurania colombica* (Bourcier), Violet-crowned Woodnymph, including subspecies *townsendi, venusta* and *colombica* recognized by Peters (1945), Guatemala and Belize south to western Panama, and disjunctly in northwestern interior Colombia (Magdalena Valley and Sierra de Santa Marta area) and adjacent northwestern Venezuela, exclusive of the range of the next form, and (3) *Thalurania fannyi* (De Lattre and Bourcier), Green-crowned Woodnymph, including subspecies *subtropicalis, fannyi, verticeps* and *hypochlora,* from eastern Panama (both slopes of Darién) southward continuously in Cauca Valley, in western Colombia (Choco) to northernmost Ecuador (Pichincha), and in western Ecuador (Provincia del Oro). In need of further study is the taxonomic status of the subspecies *hypochlora* of western Ecuador, as well as populations in the *furcata* complex.

Evolutionary implications.—The *Thalurania* woodnymphs present a fascinating mosaic of plumage characters. Relative stasis alternates with abrupt change as one moves through the range of the genus (Fig. 2). Because male plumages of hummingbirds are probably targets of sexual selection (West-Eberhard 1983), the extreme variation in plumage characters in this group may be a consequence of interactions between sexual selection and genetic drift (e.g., Lande 1980). Studies of female preferences and male characters in abrupt and gradual transition zones in woodnymphs might provide an interesting test case for this body of theory.

Studies of geographic variation in Neotropical birds have documented a recurrent pattern of "leapfrog" geographic variation in which populations at the extremes of a species range are more similar to each other than to intermediate populations (Remsen 1984, Fjeldså 1985). This pattern suggests that peripheral populations have retained ancestral characters, whereas intermediate populations have evolved derived states. In *Thalurania,* much of the geographic variation in plumage coloration can be interpreted as a series of leapfrog patterns. However, further exploration of patterns of plumage evolution in this genus in South America based on phylogenetic analysis would be most rewarding.

The richness and high endemicity of the Chocó area of Colombia and eastern Panama have been noted (e.g., Chapman 1917, Haffer 1974). In other vertebrate groups, the pattern of differentiation between Chocoan humid tropical groups and the adjacent populations from arid tropical western Panama and northern Colombia is usually described as a "broken X," in which the similarity between these latter populations is interrupted with differentiated Chocoan forms (e.g., Dunn 1940, Myers 1972). Woodnymphs fit this pattern perfectly, although only few other avian examples have been described in detail (Chapman 1917, Griscom 1932, Cracraft and Prum 1988).

Conservation status.—To our knowledge, the conservation status of woodnymphs in Middle America is of moderate concern. The Mexican populations are restricted in distribution. The area of their habitat has been reduced in recent decades, but their habitat is still fairly extensive and the woodnymphs are common within the proper forest types. Central American woodnymphs are found only in lowland forest which is increasingly endangered throughout; hence, woodnymph populations, like those of many other species, are endangered along with their habitat.

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APPENDIX I.

A: 1: Mexico, Nayarit, Palapita, 18 km S Jalcocotán (2 specimens). 2: Mexico, Nayarit, 10 km Ejido Las Mesillas (1). 3: Mexico, Jalisco, Pto. Vallarta, 1.6 mi. NE, 1 mi E

Guapinole (1). 4: Mexico, Jalisco, San Sebastian (1). 5: Mexico, Jalisco, El Refugio, Zuchitlán, 1 mi N Chimo Rd. (2). 6: Mexico, Jalisco, La Cumbre, 9 mi SSW Autlán (4). 7: Mexico, Jalisco, Puerto Los Mazos, Sierra de Manantlán (3). 8: Mexico, Colima, Puerto Juárez, La Media Luna; and La Zacatosa (4). *B:* 9: Belize, Toledo District, 7 mi NW San Pedro Columbia (1). 10: Guatemala, Gualán (1). 11: Guatemala, Izabal, Escobas; and Río Zarco (2). 12: Honduras, La Leona, Copán (1). 13: Honduras, Lombardía (1). 14: Honduras, Atlántida, San Alejo, 10 mi W Tela (3). 15: Honduras, Lancetilla (2). 16: Honduras, Las Peñitas (3). 17: Honduras, Yaruca (1). 18: Honduras, Olancho, 5 mi S San Esteban (1). 19: Honduras, Catacombas (6). 20: Honduras, Segovia River (1). 22: Nicaragua, Comarca del Cabo, 20 km SSW Waspam (4). 23: Nicaragua, Eden Mine Hill (6). *C:* 21: Nicaragua, Rió Coco/Wanks River (3). 24: Nicaragua, Zelaya, Cum, 45 km WSW Siuna (1). 25: Nicaragua, Los Sábalos, San Juan River (2). 26: Nicaragua, Savala Mata (5). 27: Nicaragua, Zelaya, El Recreo, 16 km W Rama (8). *D:* 28: Costa Rica, Aquinares (2). 29: Costa Rica, Carrillo (10). 30: Costa Rica, Bonilla (5). 31: Costa Rica, Guayabo (9). *E:* 32: Costa Rica, Barranco Boruca (5). 33: Costa Rica, El General (4). 34: Costa Rica, Jiménez (2). 35: Panama, Prov. Bocas del Toro, Zegla, Terebe River (1). 36: Panama, Almirante (1). *F:* 37: Panama, Veraguas, Rió Calovevora; and Chitra (10). 38: Panama, Gatún (5). *G:* 39: Panama, San Blas, Puerto Obaldia (11). 40: Panama, Perme (4). 41: Panama, Piñas Bay (2). 42: Panama, Mt. Sapo (2). *H:* 43: Colombia, Nariño, Buenavista (5). *I:* 44: Colombia, Huila, San Agustín (8). *J:* 45: Colombia, La Concepción (4). 46: Colombia, San Francisco (4). 47: Colombia, San Miguel (3). 48: Colombia, Santa Marta (4).

COLOR PLATE

The frontispiece painting by Sophie Webb has been made possible by an endowment established by George Miksch Sutton.

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THE BIRDS OF LONG ISLAND, BAHAMAS

DONALD W. BUDEN[1]

ABSTRACT.—One hundred and ten species of birds are recorded from Long Island and adjacent cays, 54 for the first time. No species or subspecies is endemic. Of the 48 probable breeding indigenous species, 23 are land birds, most of which are widely distributed in all terrestrial habitats. The Yellow Warbler (*Dendroica petechia*) shows the strongest habitat preference, being nearly confined to mangroves. Nests, eggs, and young are reported for 31 species, 19 of them for the first time on Long Island. The White-winged Dove (*Zenaida asiatica*) and Blue-gray Gnatcatcher (*Polioptila caerulea*) are new additions to the list of breeding land birds. The Bahama Mockingbird (*Mimus gundlachii*) was the most frequently encountered bird during summer 1990, followed closely by the Thick-billed Vireo (*Vireo crassirostris*). *Received 16 May 1991, accepted 5 Nov. 1991.*

The avifauna of Long Island has never been reviewed systematically, the literature consisting mainly of brief and sparsely annotated noncumulative lists of species. In nearly all cases, these earlier reports have been based on visits of only one to several days duration covering a very limited area, mainly Clarence Town and vicinity. The present report brings together all available information on the distribution of the birds of Long Island and is based in large measure on my observations throughout the island during 28 April–13 May and 6 July–12 August 1990 together with unpublished records contributed by other observers.

STUDY AREA

Long Island is located in the central part of the Bahama archipelago and is the southeasternmost island of any appreciable size on the Great Bahama Bank (Figs. 1 and 2). It is 103 km long, up to 5–6 km wide and 54 m high, and covers 448 km^2 (Ministry of Education 1985).

Much of the western shore is bordered by low scrub on sandy or rocky soils and occasionally mangrove swamps or tidal flats. Rocky cliffs about 10–30 m high are common along the eastern (windward) shore and are interspersed with rocky and sandy beaches. Rolling hills and north-south trending ridges occur throughout, with the highest elevations being in the south, between Deadman's Cay and Mortimers.

The vegetation is mainly scrub and low, xeric woodlands. Shrubs and bushes (ca 2–3 m tall) and small trees (5–6 m tall) cover large parts of the interior, with vegetation often so dense as to make travel off the roads and trails arduous. Visibility one meter above the ground is often less than ten meters. The largest trees reach heights of about 20 m and occur in small patches or are scattered throughout the scrub. The dominant trees include poisonwood (*Metopium toxiferum*), wild tamarind (*Lysiloma latisiliquum*), logwood (*Haematoxylum campechianum*), and lignum vitae (*Guaiacum sanctum*). Additionally, buttonwood (*Conocarpus erectus*), red mangrove (*Rhizophora mangle*), and black mangrove (*Avicennia*

[1] 220 Massasoit Road, Worcester, Massachusetts 01604.

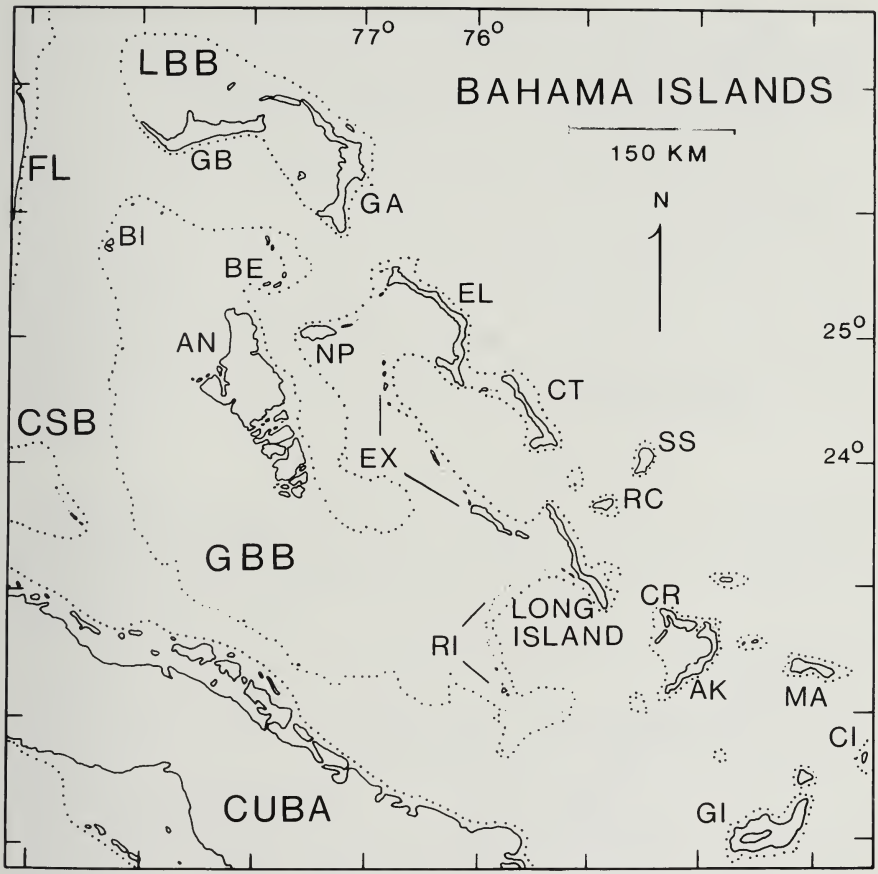

FIG. 1. Map showing the location of Long Island and other Bahama Islands; dotted lines denote the 100 fathom contour. AK = Acklins Island, AN = Andros Island, BE = Berry Islands, BI = Bimini Islands, CI = Caicos Islands, CR = Crooked Island, CSB = Cay Sal Bank, CT = Cat Island, EX = Exumas, FL = Florida, GA = Great Abaco, GB = Grand Bahama, GBB = Great Bahama Bank, GI = Great Inagua, LBB = Little Bahama Bank, MA = Mayaguana, NP = New Providence, RC = Rum Cay, RI = Ragged Islands, SS = San Salvador.

germinans) often flourish along the edges of numerous salt ponds, and casuarinas (*Casuarina equisetifolia*) are scattered along the coast, mainly on the leeward side.

Long Island falls within the tropical very dry forest category in the Holdridge system of classification, with rainfall at Clarence Town averaging 906 mm (35.7 inches) annually from 1951 to 1970, being highest during October (17.6 mm = 6.9 inches) and lowest during February and March (Little et al. 1975). There is no evidence of permanent, naturally occurring, surface freshwater (Little et al. 1975). However, between Hard Bargain and Taits, I found a sinkhole ca 30 m in diameter that contained at least a lens of freshwater and that

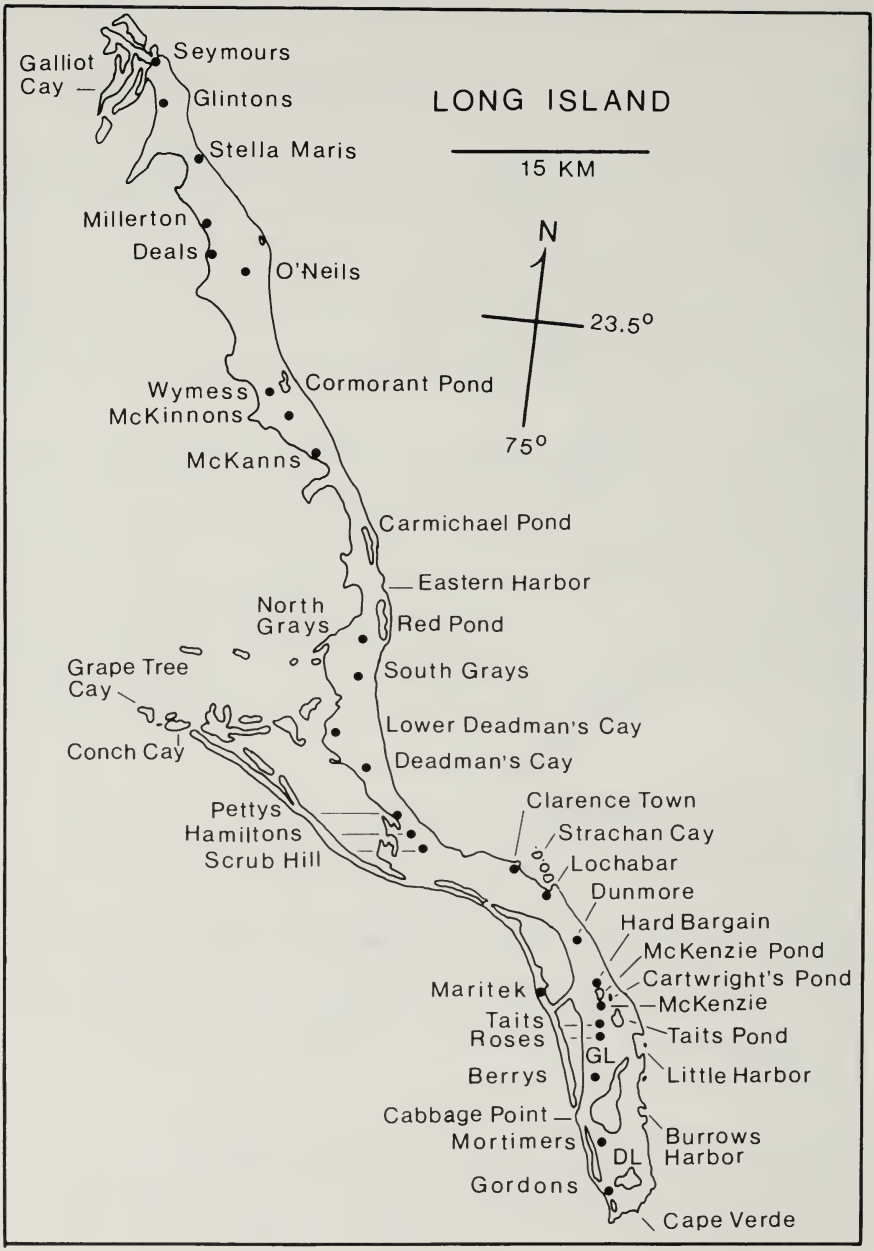

FIG. 2. Map of Long Island. DL = Deep Lake, GL = Great Lake.

was bordered by relatively luxuriant vegetation including large ferns (*Acrostichum*) and pond apple (*Annona*). Other such sinks may occur throughout the scrublands.

The total population was recorded as 3861 in the 1970 census (Ministry of Education 1985). A north-south road interconnects numerous settlements, mainly along the western coast, and many other roads and trails traverse the island. The eastern coast for the most part is uninhabited, Stella Maris and Clarence Town being the only settlements there.

The island economy is based mainly on slash and burn agriculture with numerous small farms producing crops such as tomatoes, corn, onions, cabbage, peas, mangoes, papayas, bananas, melons, and citrus for local consumption as well as shipment to Nassau. The most intensely farmed area is in the vicinity of Deadman's Cay. Sheep and goats are common throughout, and feral hogs are numerous in the southernmost part of the island. The Stella Maris Inn and Estate at the northern end of the island is a major tourist center, but the tourist industry remains undeveloped in the south where there are only a few very modest guest houses or inns. The Diamond Crystal Salt Company operated a solar evaporation salt processing plant near Hard Bargain until 1983. The salt ponds now belong to Maritek Bahamas Ltd. and are managed for commercial production of shrimp and fish.

ORNITHOLOGICAL HISTORY

Moore (1877) provided the first records of birds from Long Island in the brief accounts of his observations of Lesser Golden Plover (*Pluvialis dominica*), Bonaparte's Gull (*Larus philadelphia*), and Gull-billed Tern (*Sterna nilotica*) on 6 August and 8 October 1876. He reported that examples of the plover and tern were "killed" but gave no indication as to the disposition of any specimens.

Cory (1880) reviewed the Bahama avifauna, drawing in large measure on personal observations from 25 December 1878 to at least 25 June 1879 when he visited many islands throughout the archipelago. His statement (Cory 1880:132) "While at Clarence Harbor, Long Island a fine adult Hawk [=Osprey] came regularly every evening and perched himself upon the tip of the mainmast . . ." suggests he was there at least several days. Although the only records he specified as to date therein are all 7 June, the range of dates for ten specimens in the Field Museum of Natural History, Chicago (FMNH) catalog is 6–11 June.

A Geographical Society of Baltimore expedition to the Bahamas was at Clarence Town and vicinity during 14–17 July 1903. The ornithological results covering observations and collections of 33 species were reported by Riley (1905a) and included in a more comprehensive list of locality records for all the bird species then known from the Bahamas (Riley 1905b). The collection was deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Worthington (*in* Todd and Worthington 1911) commented briefly on Killdeer (*Charadrius vociferus*) and Northern Mockingbirds (*Mimus polyglottos*) observed at Clarence Town on 30 January 1909 while on a Carnegie Museum Expedition to the Bahamas. J. C. Greenway was on Long Island during 22–24 February 1934 on one of the Armour-*Utowana* West Indian Expeditions (see Buden 1990a), and the six specimens of four species he collected are in the Museum of Comparative Zoology, Harvard Univ. (MCZ).

R. W. Hanlon and three associates observed and collected birds in Clarence Town and vicinity during 24 June–2 July 1954. Hanlon's (1955) report covers 24 species with notes on nests and eggs for five. Specimens he collected were deposited in the Biology Dept. of Mankato State Teachers College (now Mankato State Univ.) and the Mankato Senior High School (Minnesota), but I have been unable to determine their present whereabouts.

J. R. Miller was in the Stella Maris area with several other observers during 6–8 December 1974 and 16–28 December 1975 (Miller, in litt.). Some of his records were reported by

Bond (1978, 1980, 1982). M. H. Clench observed birds in Clarence Town and vicinity on 22 March 1976, and A. Sprunt IV visited several different localities during 14 May 1984, 28–29 September 1984, and 18–22 May 1991, their field notes being sources of many new records.

METHODS

English names and binomials follow the nomenclature of the American Ornithologists' Union (1983, 1989), but placement of the Greater Flamingo (*Phoenicopterus ruber*) follows Olson and Feduccia (1980), and *Phalacrocorax brasilianus* replaces *P. olivaceus* as the scientific name of the Olivaceous Cormorant after Browning (1989). Subspecies names are used only in selected cases and follow Bond (1956) unless indicated otherwise. Abbreviations of names of observers are AS = Alexander Sprunt IV, DL = David Lincoln, DWB = Donald W. Buden, and MHC = Mary H. Clench.

Abundance is based largely on numbers of individuals usually seen during a day in the field: VC = very common, 30 or more/day; C = common, 15–30/day; FC = fairly common, 5–15/day; UC = uncommon, 1–5 on most days, but not seen every day; S = scarce, 5–15/season; and R = rare, 1–5/season.

Residents occur year-round and breed, and summer visitors breed but are less numerous or absent in winter. Nonbreeding visitors are chiefly winter visitors or transients from continental North America, including occasional visitors or vagrants as well as species present throughout the year but not breeding. The paucity of winter records for many species is an artifact of sampling and in assigning terms of seasonal abundance, I have also considered their status on adjacent islands, relying largely on Bond (1956), Brudenell-Bruce (1975), Buden (1987a, b; 1990b), Connor and Loftin (1985), and Miller (1978).

Censuses were done by recording all birds seen and heard calling while walking along roads and trails covering 164 km during 29 April–13 May and 6 July–12 August 1990. Surveys were at different times of the day from dawn to dusk, and none of the routes was censused more than once. Distances were estimated from government maps (Lands and Surveys Department 1972).

All previous locality records are included for nonbreeding visitors as well as for rare, scarce, and uncommon residents and summer visitors and for species whose status is uncertain. A species recorded on Long Island for the first time is indicated by an asterisk.

SPECIES ACCOUNTS

Least Grebe (*Tachybaptus dominicus*).—Probably a scarce resident at ponds throughout. Several observed at Clarence Town during 14–17 July 1903 (Riley 1905a), a pair seen on a pond between Stella Maris and Glintons on 10 May, another pair at a small pond east of the Maritek airstrip on 30 July, and another on a pond near South Grays, 3 August 1990 (DWB).

Audubon's Shearwater (*Puffinus lherminieri*)*.—Two seen off the northwestern coast, one on 14 May 1984, the other on 18 May 1991 (AS).

White-tailed Tropicbird (*Phaethon lepturus*).—Probably a very local summer visitor. Several seen near cliffs at the northwestern tip of the island in May 1984 and 1991 (AS).

Brown Booby (*Sula leucogaster*)*.—Probably a rare resident. Two were

seen soaring near high cliffs at Cape Verde on 14 July 1990 (DWB). According to E. Watson (pers. comm.), a long-time resident of Gordons, boobies sometimes nest on the ledges near Cape Verde, and young birds occasionally are harvested for food.

Double-crested Cormorant (*Phalacrocorax auritus*)*.—Probably an uncommon to fairly common resident. One seen in the Clarence Town area during 21–22 March 1976 (MHC), at least 19 at Maritek 28 and 29 September 1984 (AS), and several at salt ponds throughout, along with many other cormorants unidentified as to species, all during summer 1990 (DWB). "Cormorants" also were seen at Clarence Town during 14–17 July 1903 (Riley 1905a). Breeding: Twelve nests (six with three eggs, two with two eggs, one with four, and one each with one, two, and three nestlings) 2–4 m high on the tops of red mangroves on the eastern shore of Deep Lake, 24 July 1990 (one downy young salvaged as a study skin for the USNM) (DWB).

Olivaceous Cormorant (*P. brasilianus*)*.—Status uncertain, but probably resident. Six were seen at Maritek on 29 September 1984 (AS) and a partial skeleton (USNM collection) salvaged from decomposing remains found at Maritek by G. Lipscomb on 3 May 1990 was identified as *P. brasilianus* by S. Olson.

Magnificent Frigatebird (*Fregata magnificens*).—Nonbreeding visitor. Two sight records only: one immature in flight over Clarence Town on 27 June 1954 (Hanlon 1955) and two seen on 13 May 1990 (DL).

Great Blue Heron (*Ardea herodias*)*.—Probably a nonbreeding visitor. One seen at Clarence Town during 21–22 March 1976 (MHC), multiple sightings of possibly one bird at the Maritek ponds on 2 May, 17 July, 28 July, and 1 August 1990 (DWB), and others in the Deadman's Cay area year-round, but more numerous in winter (DL).

Great Egret (*Casmerodius albus*).—Status uncertain but the paucity of sightings suggests nonbreeding visitor. An unstated number were seen in the Clarence Town area during 14–17 July 1903 (Riley 1905a), and one was collected there on 30 June 1954 (Hanlon 1955).

Snowy Egret (*Egretta thula*)*.—Status uncertain. Possibly breeding locally in small numbers. One seen at Clarence Town during 21–22 March 1976 (MHC), up to 22 together at the Maritek ponds regularly during July 1990, and five flying southward along the coast at Cabbage Point, 19 July 1990 (DWB), and 24 at Maritek during 28–29 September 1984 (AS).

Little Blue Heron (*E. caerulea*)*.—Status uncertain. Possibly breeding locally in small numbers. Three seen at Clarence Town during 21–22 March 1976 (MHC), one piebald bird between Stella Maris and Millerton on 29 April and three adults at Carmichael Pond on 10 August 1990

(DWB), and two adults and one immature at Maritek during 28–29 September 1984 (AS).

Tricolored Heron (*E. tricolor*).—Fairly common resident. Most numerous at salt ponds—at least 20 together at Maritek ponds, 28–29 September 1984 (AS). Breeding: Three or four ambulatory but flightless young in mangroves on the eastern shore of Deep Lake, 24 July 1990 (DWB).

Reddish Egret (*E. rufescens*)*.—Status uncertain, possibly breeding. Two white morphs were seen between Stella Maris and Millerton on 29 April, another at the southern end of Cormorant Pond on 9 May, and both white and dark morphs at the Maritek ponds during July 1990, including five white and four dark together on 17 July (DWB). At least 50 were seen during 28–29 September 1984 (AS), and one dark morph was photographed at Grape Tree Cay in October 1988 (DL).

Cattle Egret (*Bubulcus ibis*)*.—Status uncertain. Possibly breeding in small numbers. Two seen at Clarence Town during 21–22 March 1976 (MHC), and singles at North Grays, Scrub Hill, Hard Bargain, McKenzie, and Mortimers in May and July 1990, and five together at a dump in Lower Deadman's Cay on 4 August 1990 (DWB).

Green-backed Heron (*Butorides striatus*).—Fairly common resident in aquatic habitats throughout and occasionally seen in scrubland far from water. Breeding: A nest with three eggs was collected on 30 June 1954 (Hanlon 1955), and another nest about 4 m high in a lignum vitae tree in scrub ca 0.5 km south of McKenzie Pond contained two downy young on 13 July 1990 (DWB).

Yellow-crowned Night-Heron (*Nyctanassa violacea*).—Fairly common resident throughout, most numerous in coastal habitats—maximum concentration, ten seen along 6.5 km of the eastern coast between McKenzie and the southern end of Little Harbor on 14 July 1990 (DWB). The most common heron during summer 1990 (DWB). Recorded previously only by Riley (1905a) and without comment. Breeding: A nest with one abandoned egg ca 2 m high in a buttonwood tree at Cartwright's Pond on 11 July, and one flightless young in an otherwise empty nest ca 2 m high in a red mangrove (and with four recently fledged young nearby) at Deep Lake on 24 July 1990 (DWB).

West Indian Whistling-Duck (*Dendrocygna arborea*)*.—Probably resident and more numerous than the number of sightings indicate. Its nocturnal habits and predilection for the more inaccessible ponds and swamps as diurnal retreats tend to make assessment of status difficult. Ca 125 seen on Hog Cay (just south of Galliot Cay) with others still arriving in groups of 3–12 "well before dark" on 20 May 1991 (AS), and three in flight over Deadman's Cay at dusk on 7 June 1991 (DL). I saw none during nearly

two months in the field, but many Long Islanders I met consider it a crop pest, especially in corn fields.

Snow Goose (*Chen caerulescens*).—Nonbreeding visitor. Bond (1950: 15) included Long Island in a list of Bahaman localities for the Snow Goose, attributing the record to Forsyth, presumably E. W. Forsyth of Nassau acknowledged in his preface (Bond 1950:ix). This record is not mentioned in earlier editions of his check-list (Bond 1940, 1945) but is included in the latest (fourth) edition without reference to Forsyth.

Green-winged Teal (*Anas crecca*)*.—Nonbreeding visitor. A male and female were seen together on a small pond at Cabbage Point, 25 November 1990 (DL), and one male banded as a young of the year in Quebec on 21 August 1965 was shot in southern Long Island on 10 October 1982 (Bird Banding Laboratory files).

White-cheeked Pintail (*A. bahamensis*).—Fairly common on ponds and lakes throughout, at least in summer. Possibly resident, but no winter records. Seen regularly in small numbers (2–15 together) during summer 1990 (DWB), 19–22 May 1991 (AS), and 14–17 July 1903 (Riley 1905a). Breeding: One adult was flushed from a nest on the ground at the base of a small white mangrove (*Laguncularia racemosa*) in a dense growth of *Salicornia* at Deep Lake, 15 July 1990 (DWB). The nest was lined with feathers and leaves and contained seven eggs which apparently were eaten later by feral pigs. Only a few scattered shell fragments were found when the site was revisited 24 July.

Blue-winged Teal (*A. discors*)*.—Nonbreeding visitor. Three were seen on a small pond east of McKinnons on 29 April 1990 (DWB), and six males and five females banded in Canada (one each from New Brunswick, Nova Scotia, and Prince Edward Island, and two from Ontario) and the northern United States (two from Minnesota and one each from Montana, Nebraska, Vermont, and Wisconsin) were recovered during 1955–1984 (Bird Banding Laboratory files). Of the nine recoveries dated as to month, three are October, two are December, and the other three are September, February, and March.

American Wigeon (*A. americana*)*.—Nonbreeding visitor. A male banded in Saskatchewan on 9 July 1957 was recovered in southern Long Island in 1959 (Bird Banding Laboratory files).

Ring-necked Duck (*Aythya collaris*)*.—Nonbreeding visitor. Bond (1950: 20, 1956:23) included Long Island in a list of locality records for *A. collaris* without further comment, and a male and female were seen together on a small pond at Cabbage Point on 25 November 1990 (DL).

Osprey (*Pandion haliaetus*).—Resident in coastal areas throughout (*P. h. ridgwayi*), and one record of a nonbreeding visitor (*P. h. carolinensis*)—

a male banded in Michigan as a flightless young on 15 July 1982, recovered 27 October 1982 (Bird Banding Laboratory files). Approximately 30–40 residents estimated during summer 1990 (DWB). Breeding: One female (MCZ 269642) was taken from a nest with one egg at "E. Booby Cay" (vicinity of Clarence Town?) on 23 February 1934 (J. C. Greenway), a nest at Maritek contained two young during spring 1989 (B. Sharfstein), and a local schoolboy told me one young was raised yearly at a nest on the eastern shore opposite North Grays. Locations of other nests active in recent years include one on the coast near Seymours (AS), two at the northern end of Galliot Cay (J. Friese), one on the eastern coast opposite McKanns (A. Knowles), one at Eastern Harbor (DL), one on the coast near Red Pond (DWB), one on Grape Tree Cay and two on Conch Cay (DL and DWB), and two at the southern tip of the island, one at Cape Verde and the other near the disused navigation beacon (DWB).

American Kestrel (*Falco sparverius*).—Uncommon resident. The first records are two seen during 6–8 December 1974 and others almost everyday during 16–28 December 1975, all in the Stella Maris area by Miller et al. (Miller, in litt). Bond (1980:10) reported these records as 1976. I saw kestrels in small numbers throughout during summer 1990, including one rufous morph (common in Cuba but rare in the Bahamas) at Hard Bargain on 9 July. Breeding: Nesting was reported by Bond 1980:3). Highly vociferous, territorial birds were seen regularly in spring in Deadman's Cay, and recently fledged young with presumed parents were there on 27 May 1989 (DL).

Merlin (*F. columbarius*)*.—Nonbreeding visitor. One seen harassing shorebirds at the Maritek ponds on 29 September 1984 (AS).

Peregrine Falcon (*F. peregrinus*)*.—Nonbreeding visitor. One seen regularly at Maritek and vicinity during December 1989–March 1990 (G. Lipscomb).

Clapper Rail (*Rallus longirostris*)*.—Probably resident in mangrove habitats throughout, and more numerous than records indicate: two seen 29 April, one on 1 May, one on 5 May, one heard calling on 10 May, and another seen on 25 July 1990 (DWB).

American Coot (*Fulica americana*)*.—Nonbreeding visitor. One seen at Clarence Town during 21–22 March 1976 (MHC) is the only record, but many Long Islanders report "coots and ducks" common in winter.

Black-bellied Plover (*Pluvialis squatarola*)*.—Nonbreeding visitor. Seen occasionally in small numbers during May and July 1990—maximum 10 together on 17 July (DWB). This and many other shorebird species that breed in North America almost certainly are more numerous in winter than summer, the paucity of winter records being an artifact of sampling.

Lesser Golden Plover (*P. dominica*).—Nonbreeding visitor. Two "killed" on 8 October 1876 (Moore 1877).

Snowy Plover (*Charadrius alexandrinus*).—Probably a scarce resident or summer visitor but breeding is undocumented. Seen occasionally along the shores of salt ponds during summer 1990 (DWB), and one collected on 16 July 1903 (Riley 1903a, 1905a).

Wilson's Plover (*C. wilsonia*).—Fairly common resident or summer visitor on beaches throughout. Breeding: A nest with three eggs on a beach at the northern end of Galliot Cay, 21 May 1991 (AS), and one adult with two flightless but cursorial young on a sandy beach just north of Burrows Harbor, 14 July 1990 (DWB).

Semipalmated Plover (*C. semipalmatus*).—Nonbreeding visitor. Seen regularly in small numbers (2–5 together) at salt ponds and beaches during summer 1990 (DWB), and one collected on 17 July 1903 (Riley 1905a).

Killdeer (*C. vociferus*).—Fairly common at shallow ponds and low-lying, sparsely vegetated wet areas in summer. The only winter record is one seen on 30 January 1908 (Worthington *in* Todd and Worthington 1911).

American Oystercatcher (*Haematopus palliatus*).—Probably an uncommon resident, but breeding undocumented and no winter records. Seen regularly (maximum eight in one day) on rocky beaches during summer 1990 (DWB), daily at the northern end of the island, 14 May 1984 and 18–22 May 1991 (AS), and five or six seen (one collected) in the Clarence Town area, 17 July 1903 (Riley 1905a).

Black-necked Stilt (*Himantopus mexicanus*).—Very common at ponds in summer, status in winter uncertain. Usually in flocks of 10–30—maximum 75 together at a small pond near Stella Maris, 28 April 1990 (DWB). Breeding: Downy young on one of the Clarence Town cays on 27 June 1954 (Hanlon 1955) and a nest with two eggs at Taits Pond on 10 July 1990 (DWB).

Greater Flamingo (*Phoenicopterus ruber*).—Former breeder now probably an occasional visitor. Allen (1956:121) reported there was a colony south of Clarence Town until sometime in the 1840s, and Riley (1905) received unconfirmed reports of breeding in a "lake near Clarence Harbor" in the early 1900s. Some of the local residents of settlements south of Clarence Town told me of occasional recent sightings, including one seen at Gordons on 26 July 1990, but I saw none during my stay.

Greater Yellowlegs (*Tringa melanoleuca*)*.—Nonbreeding visitor. Three were seen at Clarence Town during 21–22 March 1976 (MHC), up to ten together at salt ponds throughout during summer 1990 (DWB), and others during 28–29 September 1984 (AS).

Lesser Yellowlegs (*T. flavipes*)*.—Nonbreeding visitor. Seen regularly at salt ponds throughout, usually in small groups of 2–20 during summer 1990 (DWB), and others during 28–29 September 1984 (AS).

Willet (*Catoptrophorus semipalmatus*).—Fairly common on tidal flats and at salt ponds; probably resident but no winter records. Breeding: One flightless young with an adult on the shore of a mangrove-bordered pond north of Maritek on 2 August 1990 (DWB).

Spotted Sandpiper (*Actitis macularia*)*.—Nonbreeding visitor. I saw single birds along beaches and the shores of ponds regularly from 18 July until my departure on 12 August, but none during early July nor during 28 April–13 May 1990.

Whimbrel (*Numenius phaeopus*)*.—Nonbreeding visitor. Two seen flying across a pond at Maritek, 3 May 1990 (DWB).

Ruddy Turnstone (*Arenaria interpres*).—Nonbreeding visitor. Twelve seen during 21–22 March 1976 (MHC), two on one of the Clarence Town cays on 27 June 1954 (Hanlon 1955), and small flocks, usually of 5–15, during May and July–August 1990—maximum 35–40 together at Maritek on 3 May 1990 (DWB).

Red Knot (*Calidris canutus*)*.—Nonbreeding visitor. A flock of 13 seen at the Maritek ponds, 3 May 1990 (DWB).

Sanderling (*C. alba*)*.—Nonbreeding visitor. Five seen at the Maritek ponds on 28 July and three on a sandy beach east of McKenzie on 8 August 1990 (DWB).

Semipalmated Sandpiper (*C. pusilla*)*.—Nonbreeding visitor. Seen in small groups of 2–4 on 3 May, 22 July, and 7 August 1990 (DWB), and on 29 September 1984 (AS). Almost certainly much more numerous than records indicate, as many of the large flocks of unidentified shorebirds I saw during early May and July–August probably included this as well as other sandpiper species.

Least Sandpiper (*C. minutilla*).—Nonbreeding visitor. Over 50 seen during 21–22 March 1976 (MHC), seven seen and several collected on 16 July 1903 (Riley 1905a), and small flocks (maximum 25–30 together) seen occasionally during May and July–August 1990 (DWB).

Pectoral Sandpiper (*C. melanotos*)*.—Nonbreeding visitor. One seen at Deep Lake on 24 July, one at a small pond near Taits on 29 July, and another at Red Pond on 3 August 1990 (DWB).

Stilt Sandpiper (*C. himantopus*)*.—Nonbreeding visitor. Several seen and photographed at ponds near Maritek on 29 September 1984 (AS).

Short-billed Dowitcher (*Limnodromus griseus*)*.—Nonbreeding visitor. Two seen on 17 July, several on 31 July and 1 August 1990 (DWB), and several others on 18 May 1984 (AS).

Laughing Gull (*Larus atricilla*).—Common to very common at salt

ponds and along beaches, at least in summer—maximum 150–200 at a small pond east of Roses on 4 May and 75–100 regularly at the Maritek ponds during July 1990 (DWB). Possibly resident but no winter records. Breeding is undocumented but several recently fledged young at Deep Lake on 19 July 1990 almost certainly were hatched locally (DWB).

Bonaparte's Gull (*L. philadelphia*).—Nonbreeding visitor. The only record is one "closely observed" on 8 October 1876 (Moore 1877).

Ring-billed Gull (*L. delawarensis*)*.—Nonbreeding visitor. Two seen near Maritek on 28 September 1984 (AS).

Herring Gull (*L. argentatus*)*.—Nonbreeding visitor. One banded in Michigan as a recently fledged young on 2 July 1952 was recovered in January 1953 (Bird Banding Laboratory files).

Gull-billed Tern (*Sterna nilotica*).—Common summer visitor, most numerous at large, shallow salt ponds. The most numerous tern during summer 1990 (DWB). Breeding (all records are 1990 [DWB]).—Colony, 15 adults, three nests (two with one egg and one with two eggs), sandbar at Taits Pond, 2 July; several recently fledged young at Great Lake, 19 July; ca 50 empty nests consisting of shallow depressions on the ground lined with small shells, flakes of rock, and plaques of matted algae at McKenzie Pond on 6 May, and ca 50 others at a small, coastal pond northeast of O'Neils on 12 May. Approximately 30 adults were at the McKenzie site and 35–40 at O'Neils, but no eggs or young. A few shell fragments were found when the McKenzie site was revisited on 6 July, but no adults or active nests.

Royal Tern (*S. maxima*).—Status uncertain. Probably a scarce or uncommon summer visitor or resident, but breeding is undocumented. Five were seen during 21–22 March 1976 (MHC), "a few" during 14–17 July 1903 (Riley 1905a), and two on 29 September 1984 and several others on 21 and 22 May 1991 (AS). I saw four single birds at different localities in May and July and nine together at Maritek on 3 May 1990. The Maritek staff said Royal Terns are common at the ponds at times. No winter records, but many banded in the southeastern United States have been recovered on other Bahama Islands then (Bird Banding Laboratory files).

Sandwich Tern (*S. sandvicensis*).—Status uncertain. Possibly breeding in small numbers. Seen near Galliot Cay in May 1984 and 1991 (AS), at Clarence Town Harbor in June 1879 (Cory 1880:213), and 10–12 together at a pond south of Gordons on 25 July 1990 (DWB).

Roseate Tern (*S. dougallii*).—Probably a summer visitor in widely scattered colonies. "Common" in Clarence Town Harbor (specimen collected, FMNH) in June 1879 (Cory 1880:213) and reported as a confirmed breeder on the Clarence Town cays (Sprunt 1984). I saw ca 25 at the Maritek ponds on 3 May and several there on 17 July 1990, and AS considered

S. dougallii common in the Galliot Cay area in May 1984 and saw over 150 there during 18–22 May 1991.

Least Tern (*S. antillarum*).—Common summer visitor. Abundant and one collected in June 1954 (Hanlon 1955), and seen regularly (usually 10–15 together) at ponds and coastal areas throughout during summer 1990—maximum of 75 together at a pond south of Gordons on 25 July (DWB). Breeding: Colony, 10–15 adults, two single egg clutches, coastal pond northeast of O'Neils, 12 May 1990 (DWB); colony, ca 15 adults, two clutches (one with one egg, one with two), Deep Lake, 25 July 1990 (DWB).

Bridled Tern (*S. anaethetus*).—Probably a summer visitor to some of the immediately adjacent offshore cays, but no recent records. Cory (1880: 215) considered it abundant during June 1879 and collected four specimens on 9 June. He reported breeding birds and eggs in Clarence Town Harbor in early June, presumably on one of the cays.

Sooty Tern (*S. fuscata*).—Probably a common to very common visitor to many of the offshore cays, much less frequently on the main island. Breeding: Colony, ca 80 pairs plus eggs, one of the Clarence Town cays, 24 June–2 July 1954 (Hanlon 1955); colony, ca 200–300 adults plus eggs, upper beach zone at Lochabar, 23 May 1988 (no nesting during 1990) (DL); colony, ca 1500–2000 adults and many nearly fledged young, Strachan Cay, 12 July 1990 (DWB); many adults (probably part of a breeding colony) on a cay in Little Harbor observed from the main island, 21 July 1990 (DWB).

Brown Noddy (*Anous stolidus*).—Probably a summer visitor to some of the offshore cays, breeding very probable but undocumented. I saw approximately ten on Strachan Cay and several others in flight over an adjacent cay to the south on 12 July, and others off a cay in Little Harbor on 21 July 1990, and AS saw several in the Galliot Cay area on 19 and 20 May 1991. Previously recorded only by Cory (1892) without further comment.

Rock Dove (*Columba livia*)*.—Introduced. Seen occasionally and only in the vicinity of settlements during summer 1990 (DWB).

White-crowned Pigeon (*C. leucocephala*).—Fairly common in mangroves and the more heavily wooded areas, and probably on many of the offshore cays, at least in summer; status in winter uncertain. Seen regularly and usually no more than ten together during summer 1990 (DWB). Paul and Blankinship (1979) reported eight hunters shot 864 during 25–28 September 1978. Breeding: Colony, ca 100 adults, 10 nests (five with one egg, five with two eggs), Grape Tree Cay, 7 July 1990 (DWB); two nests each with one egg and two with two eggs, in mangroves at Deep Lake,

24 July 1990 (DWB); reported breeding at unspecified localities in 1978 with a hatching peak in early August (Paul and Blankinship 1979).

White-winged Dove (*Zenaida asiatica*)*.—Probably an uncommon resident, most numerous in the southern part of the island. I observed White-winged Doves singly or in small groups of two to four during May and July–August 1990, most of the sightings being south of Clarence Town. G. Lipscomb (pers. comm.) saw at least one regularly in the vicinity of the residence quarters at Maritek beginning in April and continuing into summer 1990. A caged bird belonging to a boy in McKenzie was caught initially on the floor of a garage, unable to fly in early July 1990. Breeding: A nest on top of a small (ca 1 m tall), isolated red mangrove on the eastern shore of Deep Lake contained one egg on 24 July 1990 (DWB). The Long Island population probably represents a recent colonization from the southern Bahamas where *Z. asiatica* has been recorded from Acklins, Great Inagua, and the Turks and Caicos Islands (Buden 1987a), and where it has become increasingly more numerous at least on the Turks and Caicos banks in recent years (Norton 1984, 1987). The only other Bahama records of which I am aware are sightings of singles on Grand Bahama on 14 November 1964 and 22 October 1966 (Kale et al. 1969).

Zenaida Dove (*Z. aurita*).—Fairly common resident throughout, most numerous in cultivated areas and along gravel roads. Breeding: Riley (1905a) reported a nest in a cavern in beach rock that contained two young "with the feathers just sprouting" on 17 July 1903. I found eight nests during summer 1990: one under construction on 10 July containing two eggs on 14 July, four others with two eggs each on 11, 19, and 29 July and 6 August, another with one egg on 18 July, one with one egg and a downy young on 23 July, and another empty except for an adult that flushed when approached on 31 July. Five of the eight nests were 1–5 m high in trees or shrubs. One of the three ground nests was in an eroded pocket of beach rock only a few meters from the tide line, another was at the base of a small red mangrove on the shore of a salt pond, and the other was in an excavated area where bulldozed land recently reverted to secondary growth of shrubs and grasses. The eight nests ranged from simple, natural depressions on the ground, scantily lined with twigs and leaves to well-formed shallow bowls or cups of loosely woven twigs.

Mourning Dove (*Z. macroura*).—Probably an uncommon resident throughout. Hanlon (1955) considered it common "in and about Clarence Town" during 24 June–2 July 1954. MHC saw one during 21–22 March 1976, and I saw a total of about 50 throughout in seven weeks during May and July–August 1990, no more than three at any one time. A male (USNM 189833) collected on 16 July 1903 clearly is *Z. m. carolinensis.*

Breeding: A nest with two downy young ca 2.5 m high in a wild tamarind in scrubland between Maritek and Hard Bargain, 30 July 1990 (DWB).

Common Ground-Dove (*Columbina passerina*).—Common resident, most numerous on roadsides and in gardens, yards, and other open grassy or weedy areas. Breeding: "Nests and eggs were observed" during 24 June–2 July 1954 (Hanlon 1955). I found one nest with two pinfeathered young on 7 May and six other nests during 15–29 July 1990, three each with two eggs, one with one egg, and two others empty except for an adult that flushed when approached. All seven nests were 1.5–5 m high in shrubs and trees.

Key West Quail-Dove (*Geotrygon chrysia*)*.—Probably a scarce resident, but status difficult to assess because of skulking habits and lack of tendency to flush, preferring stealthy retreat on the ground using dense vegetation for cover. One I saw at close range crossing an open trail through low, xeric, scrubby woodland southeast of Cormorant Pond on 8 May 1990 is the only record.

Cuban Parrot (*Amazona leucocephala*).—Probably a former resident, but the inclusion of *A. leucocephala* here rests on rather tenuous grounds apparently based on hearsay evidence; I do not know of any firsthand, confirmed reports. The Cuban Parrot occurs in the Bahamas now only on Great Abaco and Great Inagua but was more widespread there in the past (Gnam and Burchsted 1991). Bond (1956:73) stated it formerly occurred on Long Island but did not mention specific records. Cory (1918: 91) gave the range of *A. l. bahamensis* as "Inagua Acklin and Fortune Island (formerly also Abaco and Long Island) . . . ," his inclusion of Long Island doubtless stemming from an earlier report (Cory 1880:123) that "the natives claim . . . [parrots] also exist at Abaco and Long Island, but if this be true it is probably only in small numbers as we never met with them during our explorations of the last-named islands."

Mangrove Cuckoo (*Coccyzus minor*).—Probably an uncommon resident, but no winter records and breeding is unconfirmed. No more than six recorded in one day during summer 1990, and more often heard than seen (DWB). One was collected on 26 June 1954 (Hanlon 1955) and another during 14–17 July 1903 (Riley 1905a).

Smooth-billed Ani (*Crotophaga ani*).—Uncommon to fairly common resident. Riley (1905a) considered it "rather rare," but I saw anis throughout and regularly usually in groups of two to five during summer 1990 (DWB). Recorded also by Cory (1892) without further comment. Breeding: One adult at a nest of sticks and twigs ca 3 m high in a thorny, roadside tree at Deadman's Cay on 1 May 1990 (DWB); two adults seen with six young at a nest in Deadman's Cay on 27 August 1990 (DL);

reports of yearly nesting in Deals, usually in May and with five to seven adults tending a single nest (B. Deal).

Barn Owl (*Tyto alba*)*.—Rare resident. Although I did not see any owls during summer 1990, feathers and prey remains of *T. alba* were found in a small cave near the eastern coast opposite Hamiltons on 7 July, and additional feathers and prey remains along with shells of hatched eggs were on the floor of another cave on the eastern shore opposite Deadman's Cay on 3 August (DWB). Very few local residents queried have seen *T. alba* on Long Island, and its apparent scarcity there is surprising in view of the abundance of potential nesting sites in caves and sinkholes and food in the form of rats and mice, and of its widespread occurrence elsewhere throughout the archipelago.

Burrowing Owl (*Athene cunicularia*).—Status uncertain; vagrant or possibly rare resident. The only records are two seen in the Stella Maris area by J. R. Miller et al. on 19 and again (possibly same birds) on 26 December 1975 (Miller, pers. comm., in litt.; Bond 1982:11). I found no evidence of *A. cunicularia* during seven weeks in May and July–August 1990. That some Long Islanders refer to kestrels as owls, however, adds to the difficulty in assessing its status there.

Antillean Nighthawk (*Chordeiles gundlachii*).—Common summer visitor. Usually seen hawking for insects at dawn and dusk and frequently flushed from beach strand and sparsely vegetated or barren shores of salt ponds during the day—maximum 20 flushed in one hour on Grape Tree Cay, 7 July 1990 (DWB). Breeding: One downy young on 17 July 1903 (Riley 1903b); seven single egg clutches on 7, 14, 15, 18, 25, and two on 31 July, one recently hatched young on 14 July, one recently fledged young on 9 July, two others on 15 July, and another on 30 July 1990 (DWB). Nighthawks were present during my visit from from 28 April to 13 May but demonstrated no evidence of breeding then.

Bahama Woodstar (*Calliphlox evelynae*).—Fairly common resident. Breeding: One nest collected on 26 June 1954 (Hanlon 1955); four nests found 1–1.5 m high in shrubs and small trees, one with one egg on 24 July, one with two eggs on 6 August, and two each with two nestlings on 7 July and 6 August 1990 (DWB).

Belted Kingfisher (*Ceryle alcyon*)*.—Nonbreeding visitor. One seen on 9 May 1990 (DWB) and another on 29 September 1984 (AS).

Yellow-bellied Sapsucker (*Sphyrapicus varius*)*.—Nonbreeding visitor. The only records are one seen on 22 October 1988 and another on 9 November 1990, both in Deadman's Cay (DL), but "sapsucker holes" occur in many trees throughout (DWB).

Gray Kingbird (*Tyrannus dominicensis*).—Fairly common summer vis-

itor. Most numerous in the settlements and in the trees bordering salt ponds. Breeding: A nest with an undetermined number of eggs on 14 July 1903 (Riley 1905a); one nest with two eggs on 9 July, one with three eggs on 15 July, another with one nearly fledged young on 24 July, and one with two downy young on 10 August 1990 (DWB). All of the nests were 1–4.5 m high in trees, and three of the four I found were overhanging water.

Loggerhead Kingbird (*T. caudifasciatus*)*.—Probably vagrant. The only record is of one seen in a wild tamarind tree near the terminal building at Deadman's Cay airport, 12 August 1990 (DWB). It was observed at close range through binoculars for several minutes as it alternately perched quietly and moved silently among the branches at the mid-level of the canopy. The nearest known breeding populations occur in Cuba, ca 210 km southwest of Long Island, and on Andros, approximately the same distance to the northwest. *T. caudifasciatus* is resident in the Bahamas only on the northern pine-forested islands, including Grand Bahama, Abaco, Andros, and New Providence (Bond 1956, Brudenell-Bruce 1975).

Purple Martin (*Progne subis*)*.—Nonbreeding visitor. Five or six seen flying low over the road in Berrys on 4 May 1990 (DWB).

Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)*.—Nonbreeding visitor. Several seen on 29 September 1984 (AS).

Barn Swallow (*Hirundo rustica*)*.—Nonbreeding visitor. One seen on 6 May, and three other sightings of one, ten, and ca 20 during 9–12 May 1990 (DWB), and eight seen on 11 November 1990 (DL).

Blue-gray Gnatcatcher (*Polioptila caerulea*)*.—Probably a scarce or uncommon resident in scrub and xeric woodland, at least in the southern part of the island. I saw up to six in one day (maximum three together) during my visits in May and July–August 1990, and DL reported one on 16 October 1990, none of the sightings being north of Hard Bargain. Occurrence throughout July is suggestive of residents or summer visitors and not passage migrants. Confinement of records to the southernmost part of the island may indicate recent colonization from that direction or at least greater numbers in the southern and more arid region. Blue-gray Gnatcatchers are widespread in in the Bahamas and resident on most of the major islands (Bond 1956, Brudenell-Bruce 1975, Buden 1987a), but they remain unknown from a number of islands in the central part of the archipelago, including Eleuthera, the Exumas, Cat Island, Rum Cay, and San Salvador. Brudenell-Bruce (1975) stated *P. caerulea* was formerly resident on New Providence but is now only an "uncommon autumn passage migrant" there. To what extend other Bahama populations are at times augmented or supplanted by nonbreeding visitors from the southeastern United States or from other Bahama Islands is uncertain.

TABLE 1

INDIGENOUS, BREEDING LAND BIRDS OF LONG ISLAND IN DECREASING ORDER OF ABUNDANCE BASED ON GENERAL OBSERVATIONS AND WITH THE NUMBER OF BIRDS SEEN AND HEARD/KM DURING SURVEYS COVERING 164 KM

Species	Abundance[a]	Birds/km
Bahama Mockingbird (*Mimus gundlachii*)	VC	3.1
Thick-billed Vireo (*Vireo crassirostris*)	VC	2.9
Greater Antillean Bullfinch (*Loxigilla violacea*)	VC	2.4
Black-faced Grassquit (*Tiaris bicolor*)	C-VC	2.0
Bananaquit (*Coereba flaveola*)	C-VC	1.7
Common Ground-Dove (*Columbina passerina*)	C	1.4
Antillean Nighthawk (*Chordeiles gundlachii*)	C	0.1
Northern Mockingbird (*Mimus polyglottos*)	FC-VC	0.6
Gray Kingbird (*Tyrannus dominicensis*)	FC	0.4
Bahama Woodstar (*Calliphlox evelynae*)	FC	0.2
Zenaida Dove (*Zenaida aurita*)	FC	0.2
White-crowned Pigeon (*Columba leucocephala*)	FC	0.1
Smooth-billed Ani (*Crotophaga ani*)	UC-FC	0.2
Yellow Warbler (*Dendroica petechia*)	UC-FC	0.1
Mangrove Cuckoo (*Coccyzus minor*)	UC	0.2
Stripe-headed Tanager (*Spindalis zena*)	UC	0.2
Mourning Dove (*Z. macroura*)	UC	0.1
Black-whiskered Vireo (*Vireo altiloquus*)	UC	0.1
American Kestrel (*Falco sparverius*)	UC	0.1
White-winged Dove (*Z. asiatica*)	UC	0.0
Blue-gray Gnatcatcher (*Polioptila caerulea*)	S-UC	0.0
Key West Quail-Dove (*Geotrygon chrysia*)	S	0.0
Barn Owl (*Tyto alba*)	R	0.0

[a] VC = very common, C = common, FC = fairly common, UC = uncommon, S = scarce, R = rare; see Methods for additional explanation.

Gray Catbird (*Dumetella carolinensis*)*.—Nonbreeding visitor. One seen during 21–22 March 1976 (MHC) and another on 29 April 1990 (DWB).

Northern Mockingbird (*Mimus polyglottos*).—Fairly common to locally very common resident in the settlements and the more open, sparsely vegetated scrublands—1.9/km along the main road through the well-settled area between North Grays and Pettys on 1 May 1990 vs 0.6/km overall (see Table 1). Two males were collected by J. C. Greenway on 22 February 1934. Worthington (in Todd and Worthington 1911) reported it "common at Clarence Town" on 30 January 1909, MHC recorded 10 there during 21–22 March 1976, and Hanlon (1955) considered it a "very common bird in and about Clarence Town" during 24 June–2 July 1954. Breeding (all records are 1990 [DWB]): One nest with two pinfeathered young, 1.5 m high in a buttonwood tree at Seymours, 10 May; one nest

under construction ca 5 m high in a lignum vitae at Berrys on 15 July; one fledged young still with spotted breast at Dunmore on 27 July.

Bahama Mockingbird (*M. gundlachii*).—Very common resident throughout, though less numerous in the settlements than in the outlying scrublands and woodlands. The most frequently encountered bird during summer 1990 (DWB). Breeding: One nest under construction in Wymess on 9 May, another in Berrys on 15 July, and one nest with two eggs on the northeastern shore of Great Lake on 19 July 1990; all 0.5–4.5 m high in trees (DWB).

Pearly-eyed Thrasher (*Margarops fuscatus*).—Probably vagrant from adjacent islands to the south or east. Riley (1905a) considered it rare on Long Island in July 1903 but gave no indication as to how many were seen, possibly only one. There are no other firsthand records. Dense populations of *M. fuscatus* on Rum Cay (Buden 1990b) and San Salvador (Miller 1978) are very probable sources of individuals seen occasionally on the Great Bahama Bank on Eleuthera (including Harbour Island), Cat Island, Great Exuma, and Long Island. Breeding has never been documented on any of the Great Bank islands nor on the Little Bahama Bank where one *M. fuscatus* was seen on Abaco on 20 March 1990 (Norton 1990).

Thick-billed Vireo (*Vireo crassirostris*).—Very common resident throughout. Breeding: One nest under construction on 29 April, two nests each with one egg on 7 July, and another with one egg on 3 August 1990, all 1–2.5 m high in shrubs and trees (DWB).

Yellow-throated Vireo (*V. flavifrons*).—Nonbreeding visitor. Three seen during 6–8 December 1974, three on 16, two on 19, and one on 23 December 1975, all by J. R. Miller et al. in the Stella Maris area (Miller, in litt., Bond 1978:15).

Black-whiskered Vireo (*V. altiloquus*).—Uncommon summer visitor. Usually seen in heavily wooded areas, including dense mangrove swamps. Seen and heard occasionally during summer 1990, and no more than three in one day except for ten on 10 May (DWB). Riley (1905a) considered it common in the vicinity of Clarence Town during 14–17 July 1903.

Northern Parula (*Parula americana*)*.—Nonbreeding visitor. One seen on 1 May 1990 (DWB).

Yellow Warbler (*Dendroica petechia*).—Uncommon to fairly common resident in mangroves and immediately adjacent scrub, but breeding undocumented. Maximum concentration, 11 in 2 km along a mangrove and buttonwood bordered creek south of Maritek, 28 July 1990 (DWB). Cory (1880:57) said it was "not uncommon at Inagua and Long Island during May and June" 1879, and MHC saw five in the Clarence Town area during 21–22 March 1976.

Prairie Warbler (*D. discolor*)*.—Nonbreeding visitor. Three seen during 21–22 March 1976 (MHC), several nearly every day during 31 July–12 August 1990 (DWB), and one on 29 September 1984 (AS).

Palm Warbler (*D. palmarum*)*.—Nonbreeding visitor. One seen on 4 May 1990 (DWB) and another on 29 September 1984 (AS).

Bay-breasted Warbler (*D. castanea*)*.—Nonbreeding visitor. I saw one during a brief stop on Long Island on 7 May 1976 and another on 13 May 1990, both at Stella Maris.

Blackpoll Warbler (*D. striata*)*.—Nonbreeding visitor. One seen on 30 April 1990 (DWB).

Black-and-white Warbler (*Mniotilta varia*)*.—Nonbreeding visitor. One seen on 2 August 1990 (DWB).

American Redstart (*Setophaga ruticilla*).—Nonbreeding visitor. Three seen on 29 April 1990 (DWB), and also recorded by Cory (1892) without comment.

Ovenbird (*Seiurus aurocapillus*).—Nonbreeding visitor. One seen on 29 April 1990 (DWB), and recorded also by Cory (1892) without comment.

Common Yellowthroat (*Geothlypis trichas*)*.—Nonbreeding visitor. One seen on 30 April 1990 (DWB).

Bananaquit (*Coereba flaveola*).—Common to very common resident throughout. Breeding (all records are 1990 [DWB]): One fledged young soliciting food from an adult on 29 April, one nest with two pinfeathered young on 30 April, another with two naked hatchlings and one egg on 16 July, and one nest under construction on 24 July, all the nests being 2–3 m high in trees.

Stripe-headed Tanager (*Spindalis zena*).—Uncommon resident. Cory (1880:93) reported it "rather uncommon" in June 1879, and Hanlon (1955) saw only one during 24 June–2 July 1954. Riley (1905a), however, considered it "very common" in July 1903. I saw *S. zena* regularly and throughout in small numbers (maximum ten in one day on 26 July) during summer 1990. I found no direct evidence of breeding, but many of the males were calling from the topmost branches of the larger trees during late July and early August when both sexes were seen more frequently.

Summer Tanager (*Piranga rubra*)*.—Nonbreeding visitor. One male seen on 21 and 24 September 1990, probably same bird (DL).

Indigo Bunting (*Passerina cyanea*)*.—Nonbreeding visitor. Fifteen seen during 21–22 March 1976 (MHC) and five on 29 April and one on 10 May 1990 (DWB).

Black-faced Grassquit (*Tiaris bicolor*).—Common to very common resident, most numerous in weedy vegetation along roadsides and in the more sparsely vegetated scrublands. Breeding: Two nests each with two

eggs, both ca 2 m high (one in a tree, the other in a dense shrub) on 19 July, and another nest under construction ca 1 m high in a shrub on 6 August 1990 (DWB).

Greater Antillean Bullfinch (*Loxigilla violacea*).—Very common resident in scrublands and woodlands and one of the most frequently encountered birds during summer 1990 (DWB), but breeding is undocumented.

Savannah Sparrow (*Passerculus sandwichensis*)*.—Nonbreeding visitor. One seen on 10 May 1990 (DWB).

Northern Oriole (*Icterus galbula*)*.—Nonbreeding visitor. One male seen on 1 May 1990 (DWB) and sightings of at least one other male on 21 and 24 September 1990 (DL).

DISCUSSION

Of the 110 species of birds recorded from Long Island, at least 49 probably breed there; no species or subspecies is endemic. Excluding the introduced Rock Dove, 23 (=48%) of the breeders or probable breeders are land birds (pigeons to passerines plus one kestrel), 13 are shorebirds (Charadriiforms), three are herons and egrets, two are cormorants, two are ducks, and the remaining five are a grebe, tropicbird, booby, rail, and Osprey. Nine others that breed elsewhere in the Bahamas and possibly on Long Island (but are known only from a few records) include eight waterbirds (Audubon's Shearwater, Great Egret, Snowy Egret, Little Blue Heron, Reddish Egret, Cattle Egret, Royal Tern, and Sandwich Tern) and one land bird (Burrowing Owl). The Greater Flamingo (*Phoenicopterus ruber*) and Cuban Parrot probably were former breeders extirpated in the 1800s. Flamingos seen ocasionally in recent years presumably are nonbreeding visitors, probably from breeding colonies on Great Inagua.

Most of the land bird species are widely distributed in all terrestrial habitats, although the White-winged Dove and Blue-gray Gnatcatcher are more numerous in the more xeric and southern part of the island, and the Yellow Warbler is confined to mangroves and immediately adjacent scrub. The Northern Mockingbird is most numerous in the settlements, and the Common Ground-Dove and Black-faced Grassquit prefer open, weedy areas or low, sparse scrub, whereas the Gray Kingbird is usually seen in the tops of trees or on other tall, exposed perches. The nesting sites of the Antillean Nighthawk are invariably barren beds of rock, sand, or gravel, usually on beaches or the shores of ponds.

The White-winged Dove, and possibly also the Blue-gray Gnatcatcher, may represent recent range extensions from the southern Bahamas. Both are common, at least locally, among the southern islands, but neither is resident on immediately adjacent islands to the north, although the gnat-

catcher occurs on Andros and the Little Bahama Bank islands. Species that are otherwise widely distributed on the Great Bahama Bank but do not occur on Long Island are the Red-legged Thrush (*Turdus plumbeus*) and the Bahama Yellowthroat (*Geothlypis rostrata*), both of which are on comparably sized Cat Island, 50 km to the north. These absences may be due to habitat differences. The low, xerophytic vegetation of Long Island resembles that of the southern Bahamas more closely than that of other major islands on the Great Bank. Even many of the much smaller Exuma Cays have a more lush and verdant aspect.

Table 1 lists the indigenous land birds of Long Island in decreasing order of abundance based on general observations together with the results of census counts covering 164 km throughout the island. The only marked discrepancy between general observations and censuses is the relatively low count for the Antillean Nighthawk, which is usually inactive in full daylight when most of the counts were made.

Summer (ca mid-May to mid-August) is peak breeding time for many Bahama bird species (Buden 1987a, 1990b). During 6 July–13 August 1990, I found active nests, eggs, and young of 11 species of waterbirds and 13 land birds representing 46% and 57%, respectively, of the probable breeding species in these two categories. Of the 13 land bird species I found incubating or with nests under construction during summer 1990, the Antillean Nighthawk was the only obligatory ground nester. The White-crowned Pigeon and Zenaida Dove nested mainly in trees, occasionally on the ground, and the remaining ten (White-winged Dove, Mourning Dove, Smooth-billed Ani, Bahama Woodstar, Gray Kingbird, Northern Mockingbird, Bahama Mockingbird, Thick-billed Vireo, Bananaquit, and Black-faced Grassquit) had their nests one to several meters high in trees and shrubs. Four waterbird species (White-cheeked Pintail, Black-necked Stilt, Gull-billed Tern, and Least Tern) nested on the ground, and four others (Double-crested Cormorant, Tricolored Heron, Green-backed Heron, and Yellow-crowned Night-Heron) were found nesting only in trees. Most of the Osprey nests were on the ground on rocky promontories, occasionally in trees.

Potential threats, especially to ground nesting birds on Long Island, include feral cats, rats, and wild pigs in the southern part of the island. Although commercial development is minimal, there is some ongoing habitat loss and degradation as a result of small scale housing, road, and other construction.

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RECORDS WANTED OF VAGRANT BIRDS IN SEYCHELLES

A Records Committee has been established to collate data on birds in the Republic of Seychelles, which also includes the coral limestone atolls of the Amirantes, Providence, Farquhar and Aldabra groups. It will assess and publish records of vagrants, as well as monitoring the populations of breeding species and migrants, with the ultimate aim of producing a full check-list. The members are Ian Bullock, Chris Feare, James Ferguson-Lees (chairman), David Fisher, Ron Gerlach, John Phillips, and Adrian Skerrett (secretary), all of whom have spent much time in the islands. Past and present observations are needed of any species that have been reported less than annually. Lists are available from Adrian Skerrett, P.O. Box 336, Victoria, Mahe, Seychelles, to whom all observations should be sent.

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SUBSPECIFIC STATUS OF LEAST TERN POPULATIONS IN TEXAS: NORTH AMERICAN IMPLICATIONS

BRUCE C. THOMPSON,[1] MAUREEN E. SCHMIDT,[2,3] STUART W. CALHOUN,[2] DONALD C. MORIZOT,[2] AND R. DOUGLAS SLACK[4]

ABSTRACT.—Analyses of seven bill, leg, wing, and plumage characters measured from 267 museum specimens of adult Least Terns (*Sterna antillarum*) revealed significant morphological differences between sexes but not among three subspecies (*antillarum, athalassos,* and *browni*) currently recognized in North America. While individual morphometric characters sometimes did not overlap between a pair of subspecies, discriminant analysis employing criteria developed from the complete morphometric data set correctly classified >90% of *antillarum* specimens but misclassified 39% and 51% of *athalassos* and *browni* specimens, respectively. Cluster analysis did not segregate specimens into groups consistent with current subspecific taxonomy. Electrophoretic variation in proteins encoded by 50 loci revealed no genetic distinctions between *S. a. antillarum* and *S. a. athalassos* for 22 specimens from four breeding sites on the Texas coast, Rio Grande, and Texas panhandle rivers. These data illustrated continued difficulty in distinguishing endangered and nonendangered "forms" of the same species. Distinctions proposed in original descriptions of North American Least Tern subspecies are not sufficiently definitive; we recommend reassessment of subspecies within the entire species taxon. *Received 20 May 1991, accepted 22 Oct. 1991.*

Three subspecies of Least Terns (*Sterna antillarum,* formerly *S. albifrons*) are recognized from North America (A.O.U. 1957, 1983). Coastal Least Terns (*S. a. antillarum*) nest along the Atlantic seaboard from southern Maine (Hunter 1975) to Florida, the Gulf Coast, and Caribbean islands (A.O.U. 1957, 1983). Interior Least Terns (*S. a. athalassos*) breed in the Mississippi Valley; along tributaries of the Missouri, Arkansas, and Red rivers from North Dakota to Texas; and at scattered sites in the Rio Grande drainage of New Mexico and Texas (Hardy 1957, Downing 1980, Whitman 1988). California Least Terns (*S. a. browni*) are restricted to a breeding range along the Pacific Coast from San Francisco Bay, California, to Baja California, Mexico (California Least Tern Recovery Team 1980).

Number and size of *S. antillarum* breeding populations have declined in recent times owing to disturbance or destruction of nesting and feeding habitat by shoreline development, dredging, diversion and impoundment

[1] Texas Parks and Wildlife Dept., 4200 Smith School Road, Austin, Texas 78744. (Present address: U.S. Fish and Wildlife Service, New Mexico Cooperative Fish and Wildlife Research Unit, Box 30003, Dept. 4901, Las Cruces, New Mexico 88003.
[2] The Univ. of Texas M. D. Anderson Cancer Center, Science Park-Research Division, P.O. Box 389, Smithville, Texas 78957. (Present address SWC: Dept of Biology, State Univ. College at Buffalo, 1300 Elmwood Ave., Buffalo, New York 14222).
[3] Genetic Analyses, P.O. Box 598, Smithville, Texas 78957.
[4] Dept. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, Texas 77843.

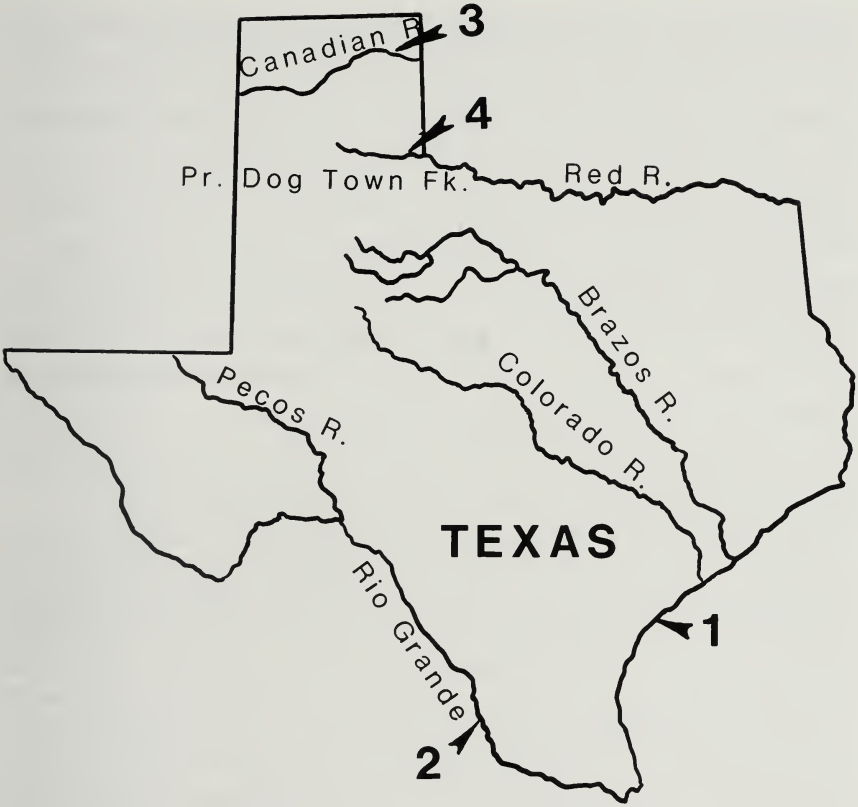

FIG. 1. Collecting localities for samples of Least Terns (*Sterna antillarum*) in (1) Aransas, (2) Zapata, (3) Hemphill, and (4) Childress counties, Texas. Samples from locality (1) represent Coastal Least Terns (*S. a. antillarum*); the remaining samples are referable to Interior Least Terns (*S. a. athalassos*).

of rivers, and recreational activities (e.g., Downing 1973, 1980; California Least Tern Recovery Team 1980; Ducey 1981; Gochfeld 1983). Endangered classification was implemented in 1970 for *S. a. browni* (U.S. Fish and Wildl. Serv. 1970) and in 1985 for *S. a. athalassos* (U.S. Fish and Wildl. Serv. 1985). Surveys during the mid-1980s estimated fewer than 2000 *S. a. athalassos* in breeding populations throughout the Mississippi River and Rio Grande drainages (summarized in Whitman 1988).

Texas is unique in supporting substantial breeding populations of two subspecies of Least Terns. Coastal Least Terns, although nesting in areas subject to disturbance by humans, are relatively abundant along the Gulf Coast, while Interior Least Terns occur in limited numbers along the Red and Canadian rivers (Fig. 1) of the Texas Panhandle (Downing 1980,

Texas Colonial Waterbird Society 1982). Least Terns also nest along the lower Rio Grande (Fig. 1) at Amistad (Val Verde Co.) and Falcon (Zapata Co.) reservoirs and near Laredo (Webb Co.), Texas. These latter birds are considered to represent *S. a. athalassos* by virtue of riverine nesting habitat and geographic inclusion in endangered classification (U.S. Fish and Wildl. Serv. 1985) but exist in closer proximity to Coastal Least Tern populations than to other populations of Interior Least Terns. Accurate taxonomic assignment of lower Rio Grande populations is important to assessments of population levels for the endangered Interior Least Tern (e.g., Downing 1980, Ducey 1981, Texas Colonial Waterbird Society 1982, Whitman 1988). Ability to distinguish subspecies through robust taxonomic criteria is important to developing conservation strategies for endangered taxa (Avise and Nelson 1989). Development of conservation and enforcement strategies related to differential classification of *antillarum* and *athalassos* under state and federal laws exemplified a need to apply more modern techniques in evaluating taxonomic status.

Difficulties in discriminating among subspecies of *S. antillarum* were exacerbated by absence of quantitative analyses of bill, wing, and leg measures in original subspecies descriptions. Indeed, suggested diagnostic characters for *S. a. browni* (Mearns 1916) and *S. a. athalassos* (Burleigh and Lowery 1942) comprised subtle differences in coloration of plumage (upperparts and nape) and bills. Specifically, Mearns (1916) described *S. a. browni,* in comparison with *S. a. antillarum,* as (1) smaller (not definitively quantified), (2) black of crown more prolonged backward, (3) usually three black outer primaries, (4) dorsum darker gray and venter more grayish, and (5) bill more narrowly tipped with black, often without any black. Burleigh and Lowery (1942) disputed the distinction of *S. a. browni* from *S. a. antillarum* and reported that *S. a. athalassos* differed from *S. a. antillarum* only in having "much darker coloration of the upper parts" and having "little or no distinction between color of the back and that of the hind neck." Number of dark primary feathers, considered by Mearns (1916) as a good character with which to distinguish *S. a. browni* (usually three) from *S. a. antillarum* (two), later was reported as highly variable among individuals of each subspecies (Burleigh and Lowery 1942). Furthermore, courtship, nesting behavior, and vocalizations are similar in Least Terns from Atlantic and Pacific coasts (Massey 1976), and behavior and habitat use characteristics are similar for coastal and interior populations (Hardy 1957, Downing 1980, Boyd and Thompson 1985, Whitman 1988). Subspecific taxonomy of Least Terns hinged on separate breeding ranges, but such a distinction was vague in the case of the Rio Grande population and meaningless for terns in migration.

We examined patterns of variation in eight bill, leg, wing, and plumage

characters among specimens of *S. a. antillarum, S. a. athalassos,* and *S. a. browni* to test hypothesized differences among subspecies and if validated, to develop criteria with which to distinguish the subspecies under field conditions. In addition, we surveyed electrophoretic variation in proteins among samples of *S. a. antillarum* and *S. a. athalassos* from nest sites along the Texas Gulf Coast, lower Rio Grande, and in the Texas Panhandle. Analyses were designed to test for discrete biochemical markers which might serve to distinguish subspecies, permit taxonomic assignment of samples from nest sites on the lower Rio Grande, and evaluate genetic consequences of small population size (decreased genetic variability and increased genetic differentiation) that may have accompanied the decline of Interior Least Terns.

MATERIALS AND METHODS

Morphological variation.—Museum specimens of *S. a. antillarum, S. a. athalassos,* and *S. a. browni* were obtained from the American Museum of Natural History, Cleveland Museum of Natural History, Field Museum of Natural History, Florida State Museum, Kansas State Museum of Natural History, U.S. National Museum of Natural History, and Texas Cooperative Wildlife Collection at Texas A&M Univ. We examined adult (breeding plumage only) specimens taken from the United States and adjacent Caribbean fringe of Mexico, Cuba, and the West Indies within the described range of the several subspecies (A.O.U. 1957, 1983). Geographic distribution was represented similarly among male and female specimens for each subspecies. Specifically, 83% of 192 *S. a. antillarum* specimens represented Gulf and Atlantic coastal sites from Texas to Massachusetts; the other 17% were collected from scattered sites in the West Indies and Gulf Coast of Mexico/Central America. All 36 *S. a. athalassos* specimens were from sites at least 250 km interior from coastal areas and represented states from Texas and Louisiana to Kansas in the Mississippi River drainage. The 39 *S. a. browni* specimens were 90% from California and 10% from the west coast of Mexico.

Date, location of collection, sex, and subspecific designation were recorded from specimen tags. Measurement of external characteristics followed Baldwin et al. (1931) and included: CULMEN—length of exposed culmen (from point at which feathers cease to hide the culmen to the culmen tip); MANDIBLE—length of lower mandible from gonys to mandible tip; TARSOTAR—diagonal of tarsus length (distance between tibiotarsal-tarsometatarsal joint and last undivided scute); MIDTOE—length of middle toe minus claw; and WINGCHOR—chord of closed folded flattened wing. Wings were measured with a millimeter ruler; all other external characters were measured with vernier calipers (accurate to 0.1 mm). The number of dark distal primaries on each wing (PRIMARYR and PRIMARYL) and presence of bill tip coloration were noted because these were important characters in original subspecies descriptions.

Relative reflectance of the mid-region of the back of each specimen was quantified by comparison with a Kodak Reflection Density Guide. This standard guide was graduated in 24 steps (or patches) that varied from white (0.0) to black (2.0). Each specimen was viewed independently by four observers under the same lighting conditions and scored by determining closest match between scale patch and specimen back reflectance (or coloration). Four scores for each specimen were averaged to produce a composite reflectance value (DENSITY).

We subjected complete records for 267 adult specimens to factorial analysis of variance (ANOVA), discriminant analysis, and cluster analysis (SAS Inst., Inc. 1982). Univariate summary statistics were calculated, and two-factor ANOVA was performed for all morphometric variables to examine individual character traits between sexes and among presumed subspecies. Scheffe's test (Zar 1974:159) was used for means separation. Normality of variables was verified with the *D* statistic of PROC UNIVARIATE (SAS Inst., Inc. 1982). Only dark primary counts and plumage reflectance values deviated significantly from normality, but transformation did not change variance pattern, so analyses were performed with original variables to preserve the scale. Stepwise discriminant analysis was used to select morphometric characters that were most efficient in separating sex or population categories (characters selected/retained at $P \leq 0.15$). Linear discrimination was used to develop criteria from the 267 specimens for distinguishing among the three subspecies currently recognized in North America. A fast cluster procedure (SAS Inst., Inc. 1982) was used to examine patterns in multivariate specimen groupings relative to location of specimen collection. This procedure evaluated the hypothesis that specimens of the three recognized subspecies would segregate into three clusters. At all stages of analysis, variables were evaluated to verify pooling of covariance matrices and pooling or separation of sexes.

Biochemical genetics.—Samples of *S. antillarum* (N = 22) were collected for biochemical genetic analyses from four nesting localities in Texas during the 1985 breeding season (Fig. 1). Coastal Least Terns (*S. a. antillarum*; N = 11) were collected alive from the shore of Aransas Bay near Rockport (Aransas Co.; 28°02′N, 97°02′W). Interior Least Terns (*S. a. athalassos*) were collected alive from sandbar nest sites on the Rio Grande (Zapata Co.; 28°36′N, 99°10′W; N = 7), the Canadian River (Hemphill Co.; 35°53′N, 100°15′W; N = 2), and the Prairie Dog Town Fork of the Red River (Childress Co.; 34°34′N, 100°12′W; N = 2). With the exception of one well-feathered individual included in the Rio Grande sample (a salvage specimen found with acute hydrocephalus), specimens were prefledging chicks taken from widely separated nests within colonies. All samples of Interior Least Terns were collected under a special endangered species subpermit from the U.S. Fish and Wildlife Service regional office in Albuquerque, New Mexico.

Liver, brain, and pectoral muscle extracted from each individual immediately after sacrifice in the lab were prepared and subjected to vertical starch-gel electrophoresis according to protocols of Siciliano and Shaw (1976) and Morizot et al. (1977). Histochemical stains were prepared as described in Siciliano and Shaw (1976) and Harris and Hopkinson (1976). Products of 50 protein loci were resolved in the electrophoretic analysis (Table 1). For multilocus protein systems, loci were designated numerically in order of decreasing anodal electrophoretic mobility of isozymes. Alleles at polymorphic loci were designated alphabetically in order of decreasing anodal electrophoretic mobility of protein products.

Genic data were analyzed as single-individual genotypes with BIOSYS-1 (Swofford and Selander 1981). Heterozygosity at individual loci (h), average individual heterozygosity over all loci ($\bar{H}$), and percentage of loci polymorphic (P; 0.95 frequency criterion) were determined by direct count. Genotypic frequencies within populations were tested for conformance to Hardy-Weinberg proportions (chi-square goodness of fit; Sokal and Rohlf 1969). Chi-square contingency-table analyses tested heterogeneity of allelic frequencies among populations (Workman and Niswander 1970).

Fixation indices (F_{ST}; Wright 1978) were calculated according to Nei and Chesser (1983) as modified by Van Den Bussche et al. (1986) to gauge the amount of genetic variance attributable to differences among collecting localities. Coefficients of genetic similarity (S; Rogers 1972), genetic distance (D; Nei 1972), and unbiased genetic distance (D_u; Nei 1978) were calculated for all pairwise comparisons of populations. Phenetic relationships among populations were depicted in a dendrogram (unweighted pair-group method using arithmetic

averages; Sneath and Sokal 1973) generated from the matrix of coefficients of *D.* Standard errors of branching points in the dendrogram were calculated according to methods of Nei et al. (1985).

RESULTS

Morphometric analyses.—Univariate statistics for 267 specimens separated by sex revealed substantial overlap of *athalassos* and *browni* with *antillarum* for the eight morphological measures (Table 2). Notable deviations from this overlap were (1) minimum CULMEN measures for both sexes of *athalassos* and *browni* which were 1.2% to 5% smaller than for smallest *antillarum* of respective sexes, and (2) only one specimen, a female *athalassos,* had five dark primaries. Evaluation of bill tip coloration indicated that darkening of the bill tip was present in >75% of specimens among all subspecies and fading or patchiness of the dark coloration defied standard measurement, thus that character was not analyzed further.

Factorial ANOVA revealed clear distinctions between sexes within subspecies for all variables except MIDTOE, TARSOTAR, and WINGCHOR (F range = 11.79 to 66.83, df = 1, 261, $P < 0.001$). Therefore, sexes were separated for subsequent analyses. Despite extensive overlap, factorial ANOVA indicated that *antillarum* had longer CULMEN (F = 24.94, df = 2, 261, $P < 0.001$), *browni* had longer WINGCHOR (F = 8.01, df = 2, 261, $P < 0.001$), and DENSITY differed among all subspecies (F = 35.90, df = 2, 261, $P < 0.001$). None of these variables extensively distinguished individual specimens to a single subspecies. PRIMARYL and PRIMARYR were highly correlated; therefore PRIMARYL was excluded from further analyses. Discriminant analysis correctly classified sex for >85% of males in all subspecies and for female *browni* but classified only 43% and 58% correctly for females of *athalassos* and *antillarum,* respectively. Discrimination based on CULMEN, DENSITY, and MANDIBLE (characters selected from stepwise procedures) were 92.1%, 93.5%, and 98.0% as accurate in distinguishing sex of *browni, athalassos,* and *antillarum,* respectively, as were criteria based on all variables.

Linear discrimination criteria correctly classified subspecies for 90.4% and 94%, respectively, of male and female specimens originally assigned to *antillarum,* but classified only 41% to 67% correct for *athalassos* and *browni* specimens of both sexes. Relatively high percentages of correct *antillarum* classifications and >30% of both sexes of *athalassos* and *browni* misassigned to *antillarum* indicated influence of *antillarum* characters among all presumed subspecies. Cluster analysis did not reveal segregation into three distinct groupings among specimens of three presumed subspecies (Table 3). Most specimens grouped in one to three clusters that contained a broad mix of the three subspecies. This analysis is not sensitive

TABLE 1

PROCEDURES USED TO RESOLVE ELECTROPHORETIC VARIATION IN SAMPLES OF COASTAL AND INTERIOR LEAST TERNS FROM TEXAS

Locus	E.C. No.	Symbol[a]	Tissue[b]	Buffer[c]
Aconitase 2 (mitochondrial)	4.2.1.3	CO2	M	TEB
Adenosine deaminase	3.5.4.4	ADA	M	TEB
Alcohol dehydrogenase	1.1.1.1	ADH	L	TC
Carbonic anhydrase 1	4.2.1.1	CA1	M	TEB
Carbonic anhydrase 2	4.2.1.1	CA2	M	TEB
Creatine kinase 1	2.7.3.2	CK1	B	TC
Creatine kinase 2	2.7.3.2	CK2	B	TC
Enolase	4.2.1.11	ENO	B	TC
Esterase 1 (α-naphthyl esters)	3.1.1.1	ES1	M	TEB
Esterase 2 (α-naphthyl esters)[d]	3.1.1.1	ES2	M	TEB/TC
Esterase 3 (methylumbelliferyl acetate)	3.1.1.1	ES3	M	TEB
Esterase 4 (methylumbelliferyl acetate)	3.1.1.1	ES4	M	TEB
Fumarate hydratase	4.2.1.2	FH	M	TEB
Glucose phosphate isomerase	5.3.1.9	GPI	M	TC
α-glucosidase	3.2.1.20	GAA	L	TC
Glutamate dehydrogenase	1.4.1.3	GLUD	L	TEB
Glutamic-oxaloacetic transaminase 1	2.6.1.1	GOT1	L	TC
Glutamic-pyruvate transaminase 1	2.6.1.2	GPT1	M	TEB
Glutamic-pyruvate transaminase 2	2.6.1.2	GPT2	M	TEB
Glutathione reductase 1	1.6.4.2	GSR1	L	TEB
Glutathione reductase 2	1.6.4.2	GSR2	L	TEB
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	GAPD	M	TC
Glycerate dehydrogenase	1.1.1.29	GLYDH	L	TC
Glycerol-3-phosphate dehydrogenase	1.1.1.8	GPD	L	TC
Glyoxalase 1	4.4.1.5	GLO	M	TEB
Guanine deaminase	3.5.4.3	GDA	L	TEB
Guanylate kinase	2.7.4.8	GUK	B	TEB

TABLE 1
CONTINUED

Locus	E.C. No.	Symbol[a]	Tissue[b]	Buffer[c]
Inosine triphosphatase	3.1.6.3	ITP	M	TC
Isocitrate dehydrogenase 1	1.1.1.42	IDH1	L	TEB
Isocitrate dehydrogenase 2	1.1.1.42	IDH2	L	TEB
Lactate dehydrogenase 1	1.1.1.27	LDH1	B	TC
Lactate dehydrogenase 2	1.1.1.27	LDH2	B	TC
Malate dehydrogenase 1	1.1.1.37	MDH1	M	TC
Malate dehydrogenase 2	1.1.1.37	MDH2	M	TC
Mannose phosphate isomerase	5.3.1.8	MPI	M	TEB
α-mannosidase	3.2.1.24	MAN	M	TEB
Muscle protein[e]		MP	M	TC
Nucleoside phosphorylase	3.4.2.1	NP	B	TEB
Peptidase 1 (glycyl-leucine)	3.4.11	PEP1	M	TEB
Peptidase 2 (leucyl-glycyl-glycine)	3.4.11	PEP2	M	TEB
Peptidase 3 (leucyl-glycyl-glycine)	3.4.11	PEP3	L	TEB
Peptidase 4 (leucyl-glycyl-glycine)	3.4.11	PEP4	L	TEB
Phosphoglucomutase 1	2.7.5.1	PGM1	M	TEB
Phosphogluconate dehydrogenase	1.1.1.44	PGD	M	TC
Phosphoglyceratemutase	2.7.5.3	PGAM	M	TEB
Pyruvate kinase	2.7.1.40	PK	B	TC
Superoxide dismutase 1	1.15.1.1	SOD1	L	TEB
Superoxide dismutase 2	1.15.1.1	SOD2	M	TEB
Triosephosphate isomerase	5.3.1.1	TPI	B	TEB
Uridine monophosphate kinase 1	2.7.4	UMPK1	B	TC

[a] Locus symbols follow standardized nomenclature for mapped human genes (McAlpine et al. 1987).
[b] B = brain; L = liver; M = pectoral muscle.
[c] TC = tris-citrate, pH 7.0; TEB = tris-EDTA-borate, pH 8.0 (Siciliano and Shaw 1976).
[d] Proteins encoded by $ES2^A$ and $ES2^B$ comigrated on TEB buffer but separated on TC buffer.
[e] Five zones of general protein activity were apparent from muscle on TC gels; nevertheless, because no allelic variation was observed, MP is reported as a single locus.

TABLE 2

UNIVARIATE STATISTICS FOR EIGHT PHYSICAL MEASURES FROM 267 LEAST TERN MUSEUM SPECIMENS REPRESENTING THREE PRESUMED SUBSPECIES IN NORTH AMERICA

Subspecies	Sex	Variable	$\bar{x}$	SE[a]	Minimum	Maximum	CV (%)[b]
antillarum	M	Culmen	28.2	0.13	24.4	31.3	5.1
	(N = 125)	Mandible	17.1	0.14	13.7	21.5	9.1
		Tarsotar	15.5	0.04	14.4	17.0	3.1
		Midtoe	13.2	0.05	11.8	14.4	4.1
		Wingchor	166.9	0.47	153.0	180.0	3.2
		PrimaryL	2.1	0.04	1.0	4.0	24.2
		PrimaryR	2.1	0.05	1.0	4.0	24.7
		Density	0.5	0.01	0.4	0.7	14.2
athalassos	M	Culmen	26.6	0.20	23.1	28.3	4.1
	(N = 29)	Mandible	16.3	0.19	14.1	18.2	6.4
		Tarsotar	15.3	0.08	14.5	16.1	3.0
		Midtoe	13.3	0.08	12.3	14.2	3.1
		Wingchor	167.8	0.82	157.0	177.0	2.6
		PrimaryL	2.3	0.09	2.0	3.0	20.6
		PrimaryR	2.3	0.09	2.0	3.0	20.4
		Density	0.6	0.01	0.5	0.7	7.5
browni	M	Culmen	26.8	0.25	23.8	29.3	4.9
	(N = 27)	Mandible	16.4	0.23	13.6	18.4	7.5
		Tarsotar	15.5	0.10	14.1	16.3	3.4
		Midtoe	13.2	0.08	12.2	13.9	3.1
		Wingchor	170.2	0.71	162.0	177.0	2.2
		PrimaryL	2.6	0.10	2.0	3.0	19.3
		PrimaryR	2.6	0.10	2.0	3.0	19.8
		Density	0.5	0.01	0.5	0.6	9.2

TABLE 2
CONTINUED

Subspecies	Sex	Variable	$\bar{x}$	SE[a]	Minimum	Maximum	CV (%)[b]
antillarum	F	Culmen	26.7	0.15	24.2	30.0	4.6
	(N = 67)	Mandible	16.3	0.16	13.1	20.1	8.0
		Tarsotar	15.6	0.06	14.6	16.5	2.9
		Midtoe	13.2	0.06	11.8	14.4	3.8
		Wingchor	166.4	0.52	154.0	173.0	2.5
		PrimaryL	2.3	0.07	1.0	4.0	24.1
		PrimaryR	2.3	0.07	1.0	4.0	23.8
		Density	0.6	0.01	0.4	0.7	11.6
athalassos	F	Culmen	25.8	0.50	23.9	27.6	5.1
	(N = 7)	Mandible	15.3	0.35	14.3	16.7	6.0
		Tarsotar	15.3	0.10	15.0	15.8	1.7
		Midtoe	13.2	0.24	12.2	14.0	4.9
		Wingchor	166.3	1.60	159.0	172.0	2.5
		PrimaryL	3.0	0.38	2.0	5.0	33.3
		PrimaryR	3.0	0.38	2.0	5.0	33.3
		Density	0.6	0.02	0.6	0.7	7.8
browni	F	Culmen	25.2	0.40	23.0	26.8	5.4
	(N = 12)	Mandible	15.8	0.35	13.4	17.9	7.7
		Tarsotar	15.4	0.08	15.0	15.9	1.8
		Midtoe	12.7	0.13	11.7	13.3	3.5
		Wingchor	169.6	1.22	161.0	174.0	2.5
		PrimaryL	2.7	0.14	2.0	3.0	18.5
		PrimaryR	2.6	0.15	2.0	3.0	19.9
		Density	0.6	0.01	0.6	0.7	6.3

[a] SE = standard error defined as standard deviation of the sample mean.
[b] CV = coefficient of variation; the sample standard deviation divided by the sample mean.

TABLE 3

MULTIVARIATE CLUSTER PATTERNS FOR 267 NORTH AMERICAN LEAST TERN SPECIMENS

Sex	N	Max. clusters[a]	Cluster	Percent of subspecies in cluster[b]		
				antillarum	*athalassos*	*browni*
Male	181	3	1	15.2	20.7	29.6
			2	66.4	69.0	66.7
			3	18.4	10.3	3.7
Female	86	3	1	10.5	14.3	8.3
			2	29.9	28.6	66.7
			3	59.7	57.1	25.0

[a] See text for rationale of selection for three clusters.
[b] FAST CLUSTER (SAS Inst., Inc. 1982) procedure applied to seven morphometric characters allowing for three clusters.

to detecting how many clusters may effectively categorize the tern specimens, only that the three clusters hypothesized from current subspecies descriptions were not verified.

Biochemical analyses.—Allelic variation was detected at 12 of 50 loci examined (Table 4). In general, allelic frequencies were similar among Texas populations and between "coastal" and "interior" subspecies. At least one allele was shared by each of the four populations at each polymorphic locus. Two alleles were common to all populations at ADA, and three alleles (C, D, and E) were common to all populations at NP. Greatest interpopulational variance in observed allele frequencies occurred at UMPK1. UMPK1^{B} predominated in Coastal Least Terns and the Rio Grande sample of Interior Least Terns, whereas UMPK1^{A} predominated among Interior Least Terns from Canadian and Red rivers (Table 4).

Genotypic frequencies conformed to expectations of Hardy-Weinberg equilibrium at all loci in each population sampled. Furthermore, when all individuals were grouped into a single population, genotypic frequencies deviated significantly from equilibrium proportions only at PGD ($\chi^2 = 3.942$; df = 1; $P = 0.047$). Chi-square contingency table analyses revealed significant heterogeneity in allele frequencies among the four populations of Least Terns at SOD2 ($\chi^2 = 10.23$, df = 3, $P = 0.017$) and UMPK1 ($\chi^2 = 9.48$, df = 3, $P = 0.024$). Allele frequencies were not significantly heterogeneous between the two populations of interior Least Terns from the Texas Panhandle (Canadian and Red rivers). Thus, individuals from these sites were combined into a single population (N = 4) for remaining analyses. Significantly heterogeneous allele frequencies were observed only at UMPK1 between this Panhandle population and coastal ($\chi^2 = 4.22$, df = 1, $P = 0.040$) and Rio Grande populations ($\chi^2 = 8.96$, df = 1, $P = 0.003$).

TABLE 4

ALLELE FREQUENCIES AT POLYMORPHIC LOCI AMONG FOUR TEXAS LEAST TERN POPULATIONS

Locus[a]	Allele	Coastal (N = 11)	Interior		
			Rio Grande (N = 7)	Canadian River (N = 2)	Red River (N = 2)
ADA	A	0.182	0.071	0.500	0.250
	B	0.818	0.929	0.500	0.750
ES1	A		0.071		
	B	1.000	0.929	1.000	1.000
ES2	A	0.864	0.786	1.000	0.750
	B		0.071		
	C	0.136	0.143		0.250
ES3	A		0.071		0.250
	B	1.000	0.929	1.000	0.750
MPI	A	0.045			
	B	0.955	1.000	1.000	1.000
NP	A	0.091			0.250
	B	0.045			
	C	0.273	0.286	0.250	0.250
	D	0.455	0.500	0.500	0.250
	E	0.136	0.214	0.250	0.250
PEP2	A	0.955	1.000	1.000	1.000
	B	0.045			
PEP3	B	1.000	0.929	1.000	1.000
	C		0.071		
PGD	A	0.150	0.200		0.500
	B	0.850	0.800	1.000	0.500
PGM1	A	0.955	1.000	1.000	1.000
	B	0.045			
SOD2	A	1.000	1.000	1.000	0.750
	B				0.250
UMPK1	A	0.450	0.214	0.750	1.000
	B	0.550	0.786	0.250	

[a] Loci are as designated in Table 1.

Average individual heterozygosity ($\bar{H}$) and percentage of loci polymorphic (P) were similar for each population (Table 5); values of these statistics over all individuals, considered as a single population, were $\bar{H} = 0.049$ and $P = 0.100$, respectively. High levels of heterozygosity (h) at the NP locus contributed much of the overall genetic variability in each population (Table 5). Fixation indices (F_{ST}) revealed modest levels of interpopulational differentiation at each polymorphic locus except UMPK1

TABLE 5

HETEROZYGOSITY AT THE POLYMORPHIC LOCI, AND FIXATION INDICES FOR TEXAS LEAST TERNS

Locus or statistic	Heterozygosity (h)[a]			F_{ST}
		Interior		
	Coastal (N = 11)	Rio Grande (N = 7)	Panhandle (N = 4)	
ADA	0.364	0.143	0.750	0.091
ES1	—	0.143	—	0.045
ES2	0.273	0.429	0.250	0.009
ES3	—	0.143	0.250	0.040
MPI	0.091	—	—	0.028
NP	1.000	0.714	1.000	0.012
PEP2	0.091	—	—	0.028
PEP3	—	0.143	—	0.045
PGD	0.100	0.400	—	0.028
PGM1	0.091	—	—	0.028
SOD2	—	—	0.250	0.081
UMPK1	0.300	0.429	0.250	0.279
$\bar{H}$[b]	0.046	0.051	0.055	
P[b]	0.100	0.160	0.140	
F_{ST}[b]				0.081

[a] h = Polymorphic loci heterozygosity.

[b] Average individual heterozygosity over all loci (H), percentage of loci polymorphic (P; 0.95 frequency criterion), and fixation indices (F_{ST}; Nei and Chesser 1983; Van Den Bussche et al. 1986).

(Table 5). Mean fixation index ($\bar{F}_{ST}$) indicated that variance in allele frequencies between populations accounted for only 8.1% of total genetic variance.

Coefficients of genetic similarity (S = 0.974), genetic distance (D = 0.007), and unbiased genetic distance (D_u = 0.003) among Texas Least Terns were consistent with overall genetic uniformity of populations. The estimate of D_u between Coastal Least Terns and the Rio Grande population of Interior Least Terns was 0.00, and the standard error for this value of D_u was undefined. Therefore, although Nei's (1978) coefficients of unbiased genetic distance were deemed more appropriate for comparisons among samples comprising few individuals, coefficients of genetic distance (D; Nei 1972) were used to assess phenetic relationships among the populations of Least Terns examined in this study. In the dendrogram derived from the matrix of D coefficients (Fig. 2), Coastal Least Terns and Interior Least Terns from the Rio Grande were clustered more closely than either of these populations was to the sample of Interior Least Terns from the Texas Panhandle. However, relatively large standard errors for

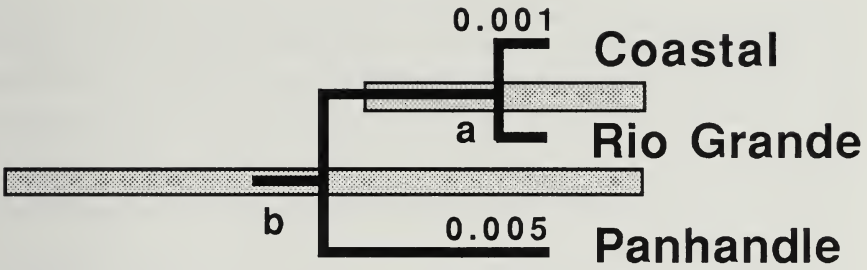

FIG. 2. Dendrogram derived from the matrix of genetic distance coefficients (*D*; Nei 1972). The "Panhandle" population represents Interior Least Terns collected from the Red and Canadian rivers in Texas (localities 3 and 4; Fig. 1). Genetic distances are expressed as the sum of branch lengths separating populations (lengths of terminal branches are shown). Shaded regions represent standard errors of branching points (calculated according to Nei et al. 1985). Standard errors for branching points denoted a and b are ± 0.003 and ±0.007, respectively.

branching points in the dendrogram indicated branch lengths separating the three populations were not different.

DISCUSSION

Bill, wing, leg, toe, and dorsum color variables used for these analyses were the same as or very similar to those reported in previous subspecies descriptions of *S. antillarum.* Individual variables showed mixed consistency with previous qualitative assessments of character differences (i.e., dorsum color but not bill tip or dark primaries in *browni,* Mearns 1916). However, multivariate discrimination did not substantiate distinction of *antillarum* from *athalassos* and *browni* as originally described by Burleigh and Lowery (1942) and Mearns (1916), respectively.

Morphometric analyses presented here seriously question existence of distinctive differences previously proposed in describing *antillarum, athalassos,* and *browni* subspecies. These analyses indicated that *antillarum* largely encompasses the range of measures inherent in North American Least Tern populations for variables examined. This similarity is consistent with Massey's (1976) suggestion that *browni* is indistinguishable behaviorally, vocally, and morphometrically from *antillarum* and Boyd and Thompson's (1985) suggestion that mixing of *antillarum* and *athalassos* may be more common than previously thought. Also, other suggested distinctions between Least Tern subspecies such as nearly mutually exclusive culmen and wing measures described by van Rossem and Hachisuka (1937) for *S. a. mexicanus* and Brodkorb (1940) for *S. a. staebleri* in Mexico relative to other subspecies including *antillarum* were not verified by measurements we report herein.

Estimated average individual heterozygosity among 22 Least Terns from Texas ($\bar{H} = 0.049$) was similar to average heterozygosity calculated by Evans (1987) from reports of biochemical genetic variation in 86 avian taxa ($\bar{H} = 0.044$). However, our estimate exceeded values estimated for Forster's Terns (*Sterna forsteri*) ($\bar{H} = 0.038$) by Hackett (1989) and for populations of California Gulls (*Larus californicus*) by Zink and Winkler (1983: $\bar{H} = 0.028$) and Karl et al. (1987: a range of $\bar{H}$ from 0.027 to 0.035). Our estimates of genetic variability in Least Terns likely were influenced by the large number of loci examined (50; Table 1) and the concomitantly large number of loci displaying allelic variation (12; Table 4). Nevertheless, our analyses did not reveal differences in levels of genetic variability among populations of Least Terns or between coastal and interior subspecies. Similarity in estimates of $\bar{H}$ and P among the three populations examined in this study suggests that genetic variability may not be declining in Interior Least Terns as a result of disruption of nesting habitat.

The only evidence for biochemical genetic differentiation among Least Tern populations from Texas involved variance in UMPK1 allele frequencies between the Panhandle samples and the remaining populations (Table 4). This variance accounted for clustering patterns in the dendrogram of genetic distance (Fig. 2) and the unusually large value of F_{ST} for this locus (0.279, Table 5). Because of small sample sizes, estimated allele frequencies at this locus, as well as others, are subject to large standard errors (± 0.106, ± 0.110, ± 0.117 for coastal, Rio Grande, and Panhandle samples, respectively). Thus, although fixation indices were estimated according to methods intended for small sample sizes (Nei and Chesser 1983), the magnitude of genetic differentiation apparent in UMPK1 allele frequencies may be illusory. We recognize that the use of more sensitive genetic techniques (e.g., analyses of restriction fragment length polymorphisms in mitochondrial DNA; Avise et al. 1987, Avise and Nelson 1989, Zink et al. 1991) or inclusion of samples of Least Terns from a larger portion of the species' range in biochemical genetic analyses (especially from the range of *S. a. browni*) might have revealed patterns of genetic differentiation that correspond with ranges of recognized subspecies. Nonetheless, observed patterns of biochemical genetic differentiation are not consistent with recognition of separate subspecies from interior (Panhandle and Rio Grande) and coastal Texas. These populations are as widely separated (>750 km) as are many of the historic breeding sites for interior and coastal populations in the Mississippi River drainage (Whitman 1988).

Lack of clearly measurable distinctions among the three subspecies, of which two are classified as endangered, complicates appropriate manage-

ment away from breeding grounds. Better understanding of migration routes, wintering areas, and extent of population mixing is necessary to determine how conservation actions directed at breeding grounds should integrate with biology and resources of these populations during the >six months they are outside the United States.

Proper conservation of endangered populations requires more information about interior populations. Additional data are needed to determine whether young fledged at "interior" colonies return there to breed; whether interior birds winter with coastal populations; and, if so, whether coastal birds are recruited into interior breeding flocks. Long-term study of young terns identifiable as to natal area is necessary to ascertain flock movements and use areas for sensitive populations. These considerations are especially warranted for isolated populations throughout the Mississippi River drainage, in the Texas Panhandle, and for the Pecos River drainage in New Mexico where only one Least Tern breeding site is known (Whitman 1988). Also, more consideration should be given to developing management strategies throughout the species range rather than just emphasizing breeding areas of uncertain subspecies.

We recommend that subspecific taxonomy of the *S. antillarum* complex be reassessed because of lack of evidence that populations are morphologically or genetically differentiated and the likelihood that populations are mixing on wintering grounds or migration routes. The subspecies concept is complex but there are compelling arguments that such categorization should at least meet minimum criteria of diagnostic morphological characters, definite geographic restriction, and ecological specialization discussed by Mayr (1970:210–213) or perhaps more importantly, reflect scientific predictiveness (Barrowclough 1982). McKitrick and Zink's (1988) review of the complexity of meaningful subspecies designations in context with current views of avian speciation is pertinent in this instance, as are the views of various authors (see Commentary on Avian Subspecies, Auk 99:593–615, 1982). Research reported here and by Massey (1976) indicated no practical means for distinction among the North American "subspecies" of Least Terns. Discrepancies in other previously suggested mensural distinctions among Least Tern subspecies further cloud the taxonomy and provide little if any predictiveness.

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WINTER HOME RANGE AND HABITAT CHARACTERISTICS OF WHITE-TAILED PTARMIGAN IN COLORADO

KENNETH M. GIESEN AND CLAIT E. BRAUN[1]

ABSTRACT.—Home ranges, habitat characteristics, and fidelity of White-tailed Ptarmigan (*Lagopus leucurus*) to wintering sites were studied in north-central Colorado. Winter home ranges of 17 hens averaged 1.62 ± 0.72 km² and were larger than those of two males (0.44 ± 0.20 km²). Home ranges of four radio-marked hens averaged 2.44 km². Percent canopy cover of willow (*Salix* spp.) was higher at ptarmigan feeding sites than at random sites when combining samples for the entire winter, but did not differ during March and April when snow depth was greatest. Crude protein of willow buds, the primary winter food, averaged 10.28% and did not differ between random and feeding sites or between fed-upon and non-used willow within a feeding site. Ptarmigan hens showed high fidelity to home ranges used in previous winters. *Received 12 April 1991, accepted 23 Oct. 1991.*

White-tailed Ptarmigan (*Lagopus leucurus*) are an important component of alpine avifaunal communities in the central and northern Rocky Mountains of North America and are one of the few resident species (Braun 1980). Previous studies of White-tailed Ptarmigan have provided information on breeding behavior and biology, population dynamics, and summer habitat characteristics (Choate 1963; Braun and Rogers 1971; May and Braun 1972; Herzog 1977; Giesen and Braun 1979a, b; Giesen et al. 1980; Hoffman and Giesen 1983; Schmidt 1988). Studies of wintering White-tailed Ptarmigan have described their habitats, migration, and flock characteristics (Braun and Schmidt 1971; Braun et al. 1976; Hoffman and Braun 1975, 1977; Herzog 1980).

We quantified home range size and documented patterns of habitat use in relation to food resources by a wintering population of White-tailed Ptarmigan in Colorado. Home range is a measure of the area used by an animal for its normal activities (Burt 1943) but may also be an index to energetic costs or habitat quality. Home range size also has implications for understanding minimum habitat patch size to sustain an individual or population.

STUDY AREA AND METHODS

We studied ptarmigan at Guanella Pass (39°35'N, 105°42'W), along the Front Range of the Rocky Mountains in north-central Colorado, during winter 1982–1983. Guanella Pass has been the site of several previous studies of White-tailed Ptarmigan (Schmidt 1969; Braun and Schmidt 1971; May and Braun 1972; Hoffman and Braun 1975, 1977) and is a willow

[1] Colorado Div. of Wildlife, 317 W. Prospect Rd., Fort Collins, Colorado 80526.

(*Salix* spp.)-dominated drainage at treeline (elevation 3475–3655 m). Approximately 10 km^2 of wintering habitat comprised the study area. This site is used each winter by 100–200 ptarmigan, primarily females (Hoffman and Braun 1977).

Climatic conditions of the Colorado Front Range have been described by Marr (1961), Judson (1965), and Marr et al. (1968) and are best characterized as continental, with wind speeds and snow depths increasing from October through late March–early April. Temperature and snowfall data were obtained from a National Oceanic and Atmospheric Administration weather station at Berthoud Pass (elevation 3448 m), approximately 23 km north. Snowfall was recorded on 139 of 211 days (65.9%) between 1 October 1982 and 30 April 1983; total snowfall for winter 1982–1983 (1233 cm) was 125% of the 15-year average. This was primarily the result of high snowfall from March to May and was not believed to have affected ptarmigan behavior or movements except for possibly delaying their departure from the wintering area. Recorded temperatures varied little from the long-term average.

We looked for ptarmigan on foot and used binoculars to scan for birds, tracks, roosts, and fecal droppings. Radio-telemetry equipment was used to locate specific birds (N = 6) and associated flocks throughout the winter. Flock size was recorded and previously captured birds were identified from their unique combinations of colored bands. Ptarmigan were classified as to age and sex following Braun and Rogers (1971); ages of birds >two years old were based on initial date of capture. Efforts were made to capture unbanded birds using wire snares on telescoping fiberglass poles (Zwickel and Bendell 1967, Braun and Rogers 1971). Locations of ptarmigan were recorded on a standardized form and later plotted on a topographic map (scale 1:24,000) to obtain Universal Transverse Mercator (UTM) coordinates to the nearest 50 m.

Three home range estimators were computed using the McPAAL software package (M. Stuwe and C. E. Blohowiak, Conserv. Res. Cent., Natl. Zool. Park, Smithsonian Inst., Front Royal, Virginia, 1985): the convex polygon method (Mohr 1947), Koeppl et al.'s (1975) 95% ellipse, and Dixon and Chapman's (1980) harmonic mean. With the harmonic mean, a 10 × 10 grid was used with a 95% estimator. Home ranges were calculated only for birds observed ≥10 times (one per day, maximum) and for those individuals initially observed prior to 25 November 1982 and with a last observation after 30 March 1983. Hoffman and Braun (1977) reported that ptarmigan began arriving on this wintering area in late October and remained until mid-April, thus most birds studied had likely spent the entire winter at Guanella Pass.

The minimum convex polygon home range estimate was used because it included all observations of birds and wasn't biased by assumptions about random movement (independent observations) of birds within their home ranges. Because it is dependent upon sample size (Jennrich and Turner 1969), it provided a conservative estimate of area used by ptarmigan in our study. The 95% ellipse assumes the most probable location of an individual is at the center of the ellipse, and the probability of observing it decreases as the ellipse increases. This method is not sensitive to sample size and assumes the animal moves randomly about its home range. The harmonic mean has been shown to be less biased (Boulanger and White 1990) but also was among the least precise. These latter two methods are based on 95% probabilities, require assumptions about home range shape, and may eliminate some locations which may be important in understanding home range or habitat use.

Willow height, height above snow, canopy cover (Canfield 1941), and snow depth were recorded at ptarmigan use and randomly selected sites within the study area. Random sites were chosen using a table of random numbers to select UTM coordinates within the wintering area. Canopy cover was measured at snowline instead of at ground level, thus canopy cover at some sites varied with snow depth. At ptarmigan use sites, plots were centered at the

greatest concentration of birds or tracks and 5-m transects were established in each of the cardinal compass directions. A 3-g sample of willow buds was collected from plants that had been fed upon and from plants not fed upon by ptarmigan at feeding sites and from willow plants at randomly selected sites. Nitrogen content of willow buds was ascertained using micro-Kjeldahl analysis (Horwitz 1980).

Mann-Whitney *U*-tests (Daniel 1978) were used to compare differences in home range sizes among classes of birds, to test for habitat differences between feeding and random sites, and to test for habitat differences among months. Differences in crude protein between fed-upon and non-fed-upon plants within sites were compared using paired *t*-tests (PROC MEANS; SAS Inst., Inc. 1988) and between feeding and random sites using *t*-tests (PROC TTEST; SAS Inst., Inc. 1988).

RESULTS

Home range size.—Forty-six of 115 ptarmigan individually identified during winter 1982–1983 were located initially prior to 25 November. Although most (N = 40, 87.0%) were observed later that winter, only 17 hens and two males were seen ≥10 times and observed at least through 31 March, thus providing minimum estimates of winter home range. The minimum convex polygon provided the most conservative estimate (Table 1) and was used for analysis. Individual winter home ranges of 17 hens averaged 1.62 ± 0.72 km^2 (mean ± SD) and were larger ($P < 0.005$) than those of two males (0.44 ± 0.20 km^2). The combined home range for the 17 hens was 7.33 km^2, or about 73% of the available winter habitat at Guanella Pass. Since these 17 hens represented <15% of the wintering population and the minimum convex polygon is a minimum home range estimate, it appears likely that most of the area was used by ptarmigan sometime during winter.

The number of observations did not appear to affect our estimates of home range among these 17 hens ($r = 0.302$, $P = 0.238$). Most (13 of 17) were located at least monthly, but there was no difference in home range size between these hens and four that were not observed every month ($P > 0.10$). Four radio-marked hens were included in the sample; these had larger home ranges than the other hens (2.44 vs 1.37 km^2; $P < 0.025$), which likely resulted from our ability to locate them after they moved to locations we seldom searched. Home range size of hens was not related to their age ($r = 0.023$, $P = 0.934$).

The minimum convex polygon provided the smallest estimate of home range. The harmonic mean estimate of average home range size for 17 hens was 45% larger, and the 95% ellipse estimate was 160% larger than the minimum convex polygon. A similar pattern was observed when using home ranges from four radio-marked hens.

Sightings of 15 adult female ptarmigan for which we calculated winter home ranges were within their individual home ranges for 100 of 114

TABLE 1
WINTER HOME RANGE ESTIMATES FOR WHITE-TAILED PTARMIGAN AT GUANELLA PASS, COLORADO, 1982–1983

Band	Age (years)	Sex	Dates observed	N obs.	Home range size (km²)		
					MCP[a]	Harmonic mean	95% ellipse
1832	12	F	09 Nov–20 Apr	37	1.43	1.95	2.42
2947	6	F	04 Nov–20 Apr	15	0.76	1.02	2.60
3259	6	F	24 Nov–15 Apr	10	2.04	3.84	9.33
3520[b]	6	F	09 Nov–15 Apr	31	3.90	6.32	9.47
3544	5	F	09 Nov–18 Apr	17	1.10	1.46	3.24
3693	5	F	21 Oct–18 Apr	32	1.34	1.57	2.49
3782	3	F	10 Nov–20 Apr	15	0.81	0.87	2.51
3786	4	F	09 Nov–18 Apr	22	1.14	1.21	3.32
3927	4	F	21 Oct–07 Apr	15	1.12	2.39	3.25
3928[b]	3	F	22 Nov–15 Apr	54	1.87	1.94	3.24
3929[b]	3	F	04 Nov–18 Apr	56	1.95	2.14	3.46
3930[b]	3	M	04 Nov–22 Apr	11	0.64	1.04	2.87
3931	3	F	09 Nov–20 Apr	34	1.62	1.94	3.04
3997	2	F	11 Oct–19 Apr	22	1.56	1.69	3.69
3999[b]	2	F	04 Nov–21 Apr	23	2.05	2.81	6.49
4096	2	F	11 Oct–31 Mar	18	1.46	2.09	4.19
4150	1	F	04 Nov–11 Apr	16	2.03	3.43	4.61
4153	1	M	16 Nov–21 Apr	12	0.24	0.39	0.95
4155	1	F	24 Nov–15 Apr	13	1.38	3.20	4.35

[a] Minimum convex polygon (Mohr 1947).
[b] Radio-marked.

observations (87.7%) during previous winters. Furthermore, 11 of these hens were identified at the Guanella Pass wintering area each year since being banded, and four were missed in only one year. It is likely these four hens were present each year also but were missed, since we spent fewer days searching for ptarmigan at Guanella Pass prior to 1982–1983.

Habitat characteristics.—Habitat characteristics were measured at 26 ptarmigan feeding sites and 21 randomly selected sites (Table 2). Because feeding sites were measured throughout winter (2 Dec–20 Apr) and randomly selected sites were measured only in March and April, direct comparison of snow depth and height of willow above snow could not be made from December to February. When comparing use sites with randomly selected sites for March and April, snow depth and willow height above snow differed in March only (Table 2).

Willow canopy cover and height above snow at feeding sites typically differed among months (Table 2) and was higher ($P = 0.0029$) at ptarmigan feeding sites than at random sites when all samples were combined. Height

TABLE 2
CHARACTERISTICS OF WHITE-TAILED PTARMIGAN FEEDING AND RANDOM SITES, GUANELLA PASS, COLORADO, 1982–1983

Month	Snow depth (cm)			Willow height above snow (cm)			Willow canopy cover (%)		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
December									
Feeding site				13.3	5.8	3	15.8[a,b]	4.0	3
January									
Feeding site	34.1	11.3	3	27.7[a]	9.6	3	37.1[a,b,c]	11.1	3
February									
Feeding site	42.8	12.6	7	26.0[b]	8.3	7	25.6[e,f]	12.1	3
March									
Feeding site	39.6*	26.1	6	8.0*[a,b]	2.9	6	8.8[a,c,e]	3.3	6
Random site	85.0	13.4	7	16.3	9.7	7	8.6	6.4	7
April									
Feeding site	72.3	23.9	7	12.4[b]	3.0	7	8.2[b,d,f]	4.3	7
Random site	86.7	21.9	14	15.3	5.3	14	6.7	4.1	14

* Means between feeding and random sites differ, Mann-Whitney test, $P < 0.05$.
[a,b,c,d,e,f] Means within a column sharing a letter are different, Mann-Whitney test, $P < 0.05$.

above snow generally decreased from January to April, which reflected increasing snow depths. Similarly, canopy cover declined during the same period, a reflection of less exposed canopy cover as snow depth increased.

Crude protein did not differ between buds from willow shrubs fed upon by ptarmigan and those nearby which were not fed upon, or those from randomly selected sites (Table 3). The overall level of crude protein was 10.28%.

DISCUSSION

Although we did not detect a significant correlation between individual winter home range size and number of observations, our data were biased by non-random distribution of ptarmigan and search patterns. Access to Guanella Pass was fortuitously adjacent to areas preferred by ptarmigan early and late in winter, and this area was searched on most trips to the area. Thus, birds that used this area were seen more often than those which dispersed throughout the wintering site. We believe the larger home ranges of radio-marked birds represent the most accurate estimate of White-tailed Ptarmigan winter home range size.

The smaller winter home ranges of the two males reflected their pref-

TABLE 3
CRUDE PROTEIN LEVELS OF WILLOW BUDS AT GUANELLA PASS, COLORADO, 1982–1983

Site	Crude protein (%)		N
	Mean	SD	
Feeding sites	10.39[a]	0.17	37
Fed-upon plants	10.46[b]	0.82	17
Non-fed-upon plants	10.35[b]	1.31	17
Random sites	10.14[a]	0.15	29

[a] Crude protein did not differ, $P = 0.2635$.
[b] Crude protein did not differ, $P = 0.7339$.

erence for different winter habitats (Hoffman and Braun 1977) and their tendency to remain in small flocks throughout winter (Braun and Schmidt 1971). This spatial and habitat segregation may reflect a strategy of males to winter adjacent to breeding territories, thus reducing competition for resources in winter habitats.

Winter home range sizes are not well documented for grouse. Reported winter home range sizes of Greater Prairie-Chickens (*Tympanuchus cupido*) range from 8.4 km^2 (Toepfer and Eng 1988) to <0.4 km^2 (Robel et al. 1970, Schroeder and Braun 1992). Winter home ranges of Blue Grouse (*Dendragapus obscurus*) were <0.2 km^2 (Cade 1985, Hines 1986) and those of Spruce Grouse (D. *canadensis*) <0.1 km^2 (Herzog and Boag 1978). If size of winter home range is related to flock size, then increased winter flock size and home range may be a consequence of open habitats and dispersed winter food resources that are spatially separate from secure roosting habitat.

Fidelity of White-tailed Ptarmigan to wintering areas has been reported previously (Braun et al. 1976, Hoffman and Braun 1977). Our data indicate White-tailed Ptarmigan also show fidelity to individual winter home ranges. The benefits of such fidelity may include knowledge of roosting and foraging sites or may confer competitive advantages through dominance when feeding.

Densities of White-tailed Ptarmigan at Guanella Pass in winter averaged 10–20 birds/km^2, which is twice their mean density on breeding ranges (Braun and Rogers 1971). However, breeding territories are defended by paired birds whereas ptarmigan in winter are typically associated with flocks of 12–21 birds (Braun et al. 1976). Flocking of grouse in winter may be advantageous for obtaining or sharing information on food distribution and may also serve as a tactic for predator detection, which may increase survival of flock members (Bergerud and Gratson 1988). Flock composition and membership constantly changed throughout the winter,

thus individual ptarmigan had contact with a large proportion of the local wintering population. Large home ranges shared with conspecifics may result in decreased costs of defending abundant and dispersed food resources and allow for use of suitable snow roosting sites, which change in response to snow and wind conditions.

Willow buds, the primary winter food of White-tailed Ptarmigan in Colorado (May and Braun 1972), were available throughout the winter at Guanella Pass. Previous studies also indicated that food quantity (gross energy) and nutrient availability were not limiting to ptarmigan on a willow diet in winter (May 1975). White-tailed Ptarmigan gain weight during the winter period (May 1975; C. E. Braun, unpubl. data), which also suggests that food is not limiting in areas they occupy.

Whether ptarmigan exercised any selection for winter food was not determined, but no selection based on crude protein was observed. Our measure of crude protein was similar to that reported previously for White-tailed Ptarmigan in winter (9.5%, May 1975) and within the range reported in the winter diets of other grouse (Hoffmann 1961, Ellison 1966, Korshgen 1966, Moss 1968, Huff 1970, Pendergast and Boag 1971, Gasaway 1976, Gurchinoff and Robinson 1972, Pulliainen 1978, Remington 1983). Andreev (1988) reported that 10% crude protein was optimal for winter diets of Palaearctic grouse.

Suitable winter habitats for White-tailed Ptarmigan appear limiting (Hoffman and Braun 1975, Braun et al. 1976, Herzog 1980), primarily because of extreme weather conditions in alpine environments and high snowfall which limits food resources. Ptarmigan have adapted to this environment by migrating to areas where food is abundant (Hoffman and Braun 1975), and adopting behaviors and seeking microenvironments to minimize energy expenditures (Braun and Schmidt 1971).

All suitable habitats at Guanella Pass appeared to be used by ptarmigan in winter; the specific areas used changed in response to snow accumulation which affected snow roosting sites and food availability and abundance (Braun and Schmidt 1971). Localized food depletion, competition with conspecifics, snowfall, and availability of suitable conditions for snow roosting may contribute to daily and monthly movements during winter.

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GREATER PRAIRIE-CHICKEN ATTENDANCE AT LEKS AND STABILITY OF LEKS IN COLORADO

MICHAEL A. SCHROEDER[1,2] AND CLAIT E. BRAUN[2]

ABSTRACT.—Greater Prairie-Chicken (*Tympanuchus cupido*) lek visitation and stability were examined in 1986–1991 on a 301-km² area in northeastern Colorado. Although 39–47 leks were active during any given year, about 23% of leks disappeared between consecutive years. Twenty of 80 leks were active all six years and 26 leks were active only one year. Relatively stable leks appeared to have greater male visitation than unstable leks. In addition, numbers of males visiting stable leks tended to be correlated with density of leks on the study area. Twenty-one radio-marked males were observed on 286 occasions during peak display periods; 95.1% of those observations were on lek sites. Rates of lek visitation were similar for adults and yearlings captured on leks or during winter. *Received 3 June 1991, accepted 20 Oct. 1991.*

Many species of Tetraoninae congregate on leks for breeding including Sage Grouse (*Centrocercus urophasianus*), Sharp-tailed Grouse (*Tympanuchus phasianellus*), Lesser Prairie-Chicken (*T. pallidicinctus*), and Greater Prairie-Chicken (*T. cupido*). Density of leks and attendance of males at leks have been used as indices of abundance of Greater Prairie-Chicken populations at many locations (e.g., Hamerstrom and Hamerstrom 1973, Horak 1985, Kobriger et al. 1988). Despite use of such indices, little is known about male attendance at leks and the stability and/or distribution of leks (Cannon and Knopf 1981).

Robel (1970) suggested that about 50% of male Greater Prairie-Chickens observed prior to the breeding season occupied territories on leks during the peak of the breeding season; presumably non-territorial males were in adjacent areas (Ballard and Robel 1974). Similarly, Rippin and Boag (1974) suggested that some male Sharp-tailed Grouse were non-territorial in areas adjacent to leks, while waiting for territories on leks to become available. However, actual locations of these 'surplus' males are difficult to determine; they may either be in areas adjacent to leks or on other leks.

Numbers of male Greater Prairie-Chickens at leks in Kansas declined throughout the breeding season (Robel 1970). In contrast, numbers of males remained relatively stable at leks in Wisconsin (Hamerstrom and Hamerstrom 1973). It is not known whether changes in lek visitation are influenced by mortality of males during the breeding season and/or changes in the likelihood of males to visit leks.

[1] Dept. of Fishery and Wildlife Biology, Colorado State Univ., Fort Collins, Colorado 80523. Present address: Washington Dept. of Wildlife, P.O. Box 1077, Bridgeport, Washington 98813.
[2] Colorado Division of Wildlife, Wildlife Research Center, 317 West Prospect Road, Fort Collins, Colorado 80526.

Adult males may form a stable territorial population while non-territorial males may be responsible for observed fluctuations in attendance of males at leks; these differences in attendance may be related to differences between "permanent" (referred to as ancestral leks by Hamerstrom and Hamerstrom [1973]) and "temporary" (referred to as "satellite" leks by Hamerstrom and Hamerstrom [1973] and "adjunct" leks by Grange [1948]). Whereas permanent leks may be active every year, temporary leks may appear and disappear during years of population fluctuations (Grange 1948, Cannon and Knopf 1981).

Counts of both leks and males have been used as indices of status of prairie grouse populations. Consequently, the objective of this research was to document the attendance of males at leks and the stability of leks in a population of Greater Prairie-Chickens. Because stability of leks may be closely related to attendance of males at leks, we examined (1) stability of leks, (2) relationships between male attendance at leks and lek stability and density, and (3) frequency of occurrence of radio-marked male Greater Prairie-Chickens at leks.

METHODS

We inventoried a 301-km^2 area 10 km northeast of Eckley, Colorado (40°11′N, 102°22′W), each year from 1986 to 1991 to estimate lek density and attendance of male Greater Prairie-Chickens (after Hamerstrom and Hamerstrom 1973). The habitat was primarily gently rolling rangeland consisting of grassland, sand sagebrush (*Artemisia filifolia*), and small soapweed (*Yucca glauca*) intermixed with irrigated cropland, primarily corn. In general, habitat on the area studied remained consistent throughout the 1986–1991 period (Schroeder and Braun 1992).

Two or more displaying males in a cluster were considered a lek. Different leks generally were separated by at least 0.5 km (or distinct topography). We conducted two complete surveys of the area each year. Attendance for each lek (within a year) was estimated using the maximum of at least two counts of males at each site. Although males on all leks were flushed and counted, leks were approached slowly in order to determine if females were present. Males at leks were counted during March and April, peak periods of male attendance at leks (Hamerstrom and Hamerstrom 1973).

Trapping was concentrated on a core area of approximately 100 km^2 during 1986–1988. Male Greater Prairie-Chickens were captured on leks, using walk-in traps (Schroeder and Braun 1991) and cannon nets, and at winter feeding sites using walk-in traps baited with corn. Thirteen adults and nine yearlings were captured on leks and seven adults and five yearlings were captured during winter. Captured males were banded with a numbered aluminum band and a unique combination of three colored plastic bands and fitted with battery- or solar-powered radio transmitters attached to poncho-type markers (Amstrup 1980). Radios weighed 1.8–2.3% of each bird's body weight. Birds were classified as yearlings (first breeding year) or adults (>first breeding year) (Ammann 1944).

Observations of radio-marked males were made between 0.5 hours before to 2.0 h after sunrise during 1 March–30 April 1986–1988; these dates were chosen to represent the normal display season for males of 15 February–15 May. Radio-marked Greater Prairie-Chickens were located by using a portable Telonics' receiver and three-element Yagi antenna. Ob-

servations consisted of visual sightings of radio-marked males on leks (usually from 0.2 to 1.0 km away) and/or triangulation (3 or more azimuths obtained ≤0.5 km of target transmitters and at angles-of-incidence >35° and <145°). Approximately 40% of the observations were obtained visually. All locations were recorded as Universal Transverse Mercator coordinates (nearest 10-m interval).

Examinations of accuracy indicated that 90% of the locations derived by triangulation were within 250 m of actual locations (Schroeder 1991). If an estimated location was within 250 m of the center of a lek, the radio-marked bird was assumed to be on the lek. There are three basic reasons why we believe these results were accurate. First, triangulation accuracy for radio-marked males was probably better than the 250-m estimate generated for radios in known locations such as nest and mortality sites (Schroeder 1991); distances between observers and radio-marked males were closer and males were in prominent locations. Second, since leks may be >250 m in diameter, these results were considered conservative. Third, radio telemetry was used to estimate locations of radio-marked males before leks were approached (when traps were checked); males estimated to be on the lek flushed with the other males on the lek.

RESULTS

Lek stability.—Eighty leks were documented on the study area during 1986–1991 (Fig. 1); single males displayed at an additional 11 locations. The number of leks ranged between 39 in 1991 and 47 in 1988. The density of leks was relatively stable at 0.14 leks/km^2 (Table 1). Numerous leks disappeared between consecutive years; eight of 41 between 1986 and 1987, 12 of 42 between 1987 and 1988, 13 of 47 between 1988 and 1989, eight of 42 between 1989 and 1990, and eight of 41 between 1990 and 1991. The average annual disappearance rate for leks was 22.9%. Twenty leks were active all six years, six for five years, seven for four years, six for three years, 15 for two years, and 26 for one year. The relatively large numbers of leks active either six years or only one year appeared to reflect a bimodal tendency in stability of leks.

Numbers of males visiting leks ranged between two and 28; density of males observed on the study area ranged between 0.98 in 1986 and 1.69 males/km^2 in 1988 (Table 1). Male attendance at individual leks was positively correlated with their stability ($r = 0.438$, $P < 0.001$, N = 252 [pooled sample]). Average attendance of males was 3.62 (SD = 1.77) at leks active one year, 6.67 (SD = 5.29) at leks active two years, 7.78 (SD = 5.06) at leks active three years, 8.57 (SD = 3.76) at leks active four years, 7.17 (SD = 3.32) at leks active five years, and 10.84 (SD = 4.90) at leks active all six years (Fig. 2).

Although total attendance of males at leks fluctuated between years, fluctuations apparently were not in response to density of leks on the study area ($r = 0.423$, $P = 0.403$). Despite small sample sizes, male attendance at relatively stable leks tended to be positively correlated with number of leks on the study area; $r = 0.713$ ($P = 0.112$) for leks active six years,

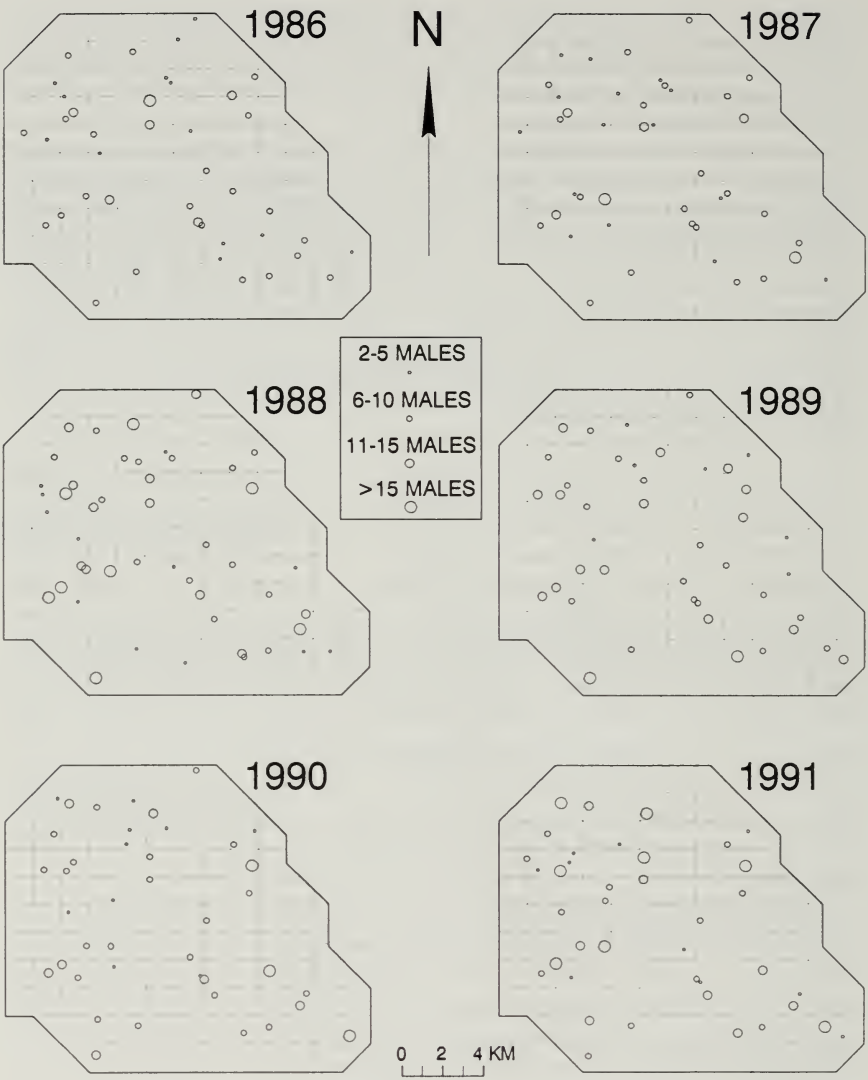

FIG. 1. Distribution of Greater Prairie-Chicken leks on a 301-km² study area in northeastern Colorado, 1986–1991. Each square represents one cadastral section (2.59 km²).

$r = 0.811$ ($P = 0.050$) for leks active five years, $r = -0.346$ ($P = 0.502$) for leks active four years, $r = 0.848$ ($P = 0.033$) for leks active three years, $r = 0.158$ ($P = 0.765$) for leks active two years, $r = 0.531$ ($P = 0.278$) for leks active one year.

Attendance of males on leks.—The average date for the maximum count

TABLE 1
INDICES OF LEK STABILITY AND ABUNDANCE OF MALE GREATER PRAIRIE-CHICKENS ON A 301-KM² STUDY AREA IN NORTHEASTERN COLORADO, 1986–1991

Index	1986	1987	1988	1989	1990	1991
Number of leks						
Active	41	42	47	42	41	39
Additional (not previously active)	—	9	15	6	5	4
Active during previous year	—	33	30	34	34	33
Disappearing during previous year	—	8	12	13	8	8
Lek density (leks/km²)	0.14	0.14	0.15	0.14	0.14	0.13
Number displaying males/lek						
$\bar{x}$	7.22	7.29	10.47	8.86	8.41	9.74
SD	3.89	4.39	5.97	3.86	4.72	5.80
Male density[a] (males/km²)	0.98	1.02	1.69	1.23	1.17	1.08

[a] Includes males displaying alone.

of males on leks was 1 April (SD = 3 days). However, examination of male attendance throughout the breeding season (late Feb–early June) indicated that attendance was relatively stable during March and April, particularly on undisturbed leks (those which were not used for trapping during the breeding season) (Fig. 3). Regardless of disturbance status, attendance appeared to decline after April.

Annual changes in attendance of males at leks may reflect either regional or local changes in lek visitation (Fig. 1). Regional changes would be characterized by a positive correlation between changes in annual attendance of males at neighboring leks (if the number of males/lek increases, the number of males/lek on the nearest neighboring lek should also increase). In contrast, local changes or "shifts" in lek visitation would be characterized by a negative correlation (if number of males/lek increases, number of males/lek on the nearest neighboring leks should decrease). Although changes were not correlated for 1986–1987 ($r = 0.062$, $P = 0.663$), 1987–1988 ($r = -0.069$, $P = 0.582$), and 1988–1989 ($r = -0.035$, $P = 0.791$), they were negatively correlated for 1989–1990 ($r = -0.230$, $P = 0.028$) and 1990–1991 ($r = -0.695$, $P < 0.001$). The relationship was not significant ($r = -0.076$, $P = 0.184$) for all years combined.

Frequency of occurrence of radio-marked males on leks.—Of 34 male Greater Prairie-Chickens fitted with radio transmitters, 13 could not be observed during the breeding season (10 died and three had radios removed). Of the remaining 21 males, 13 males with a minimum of nine

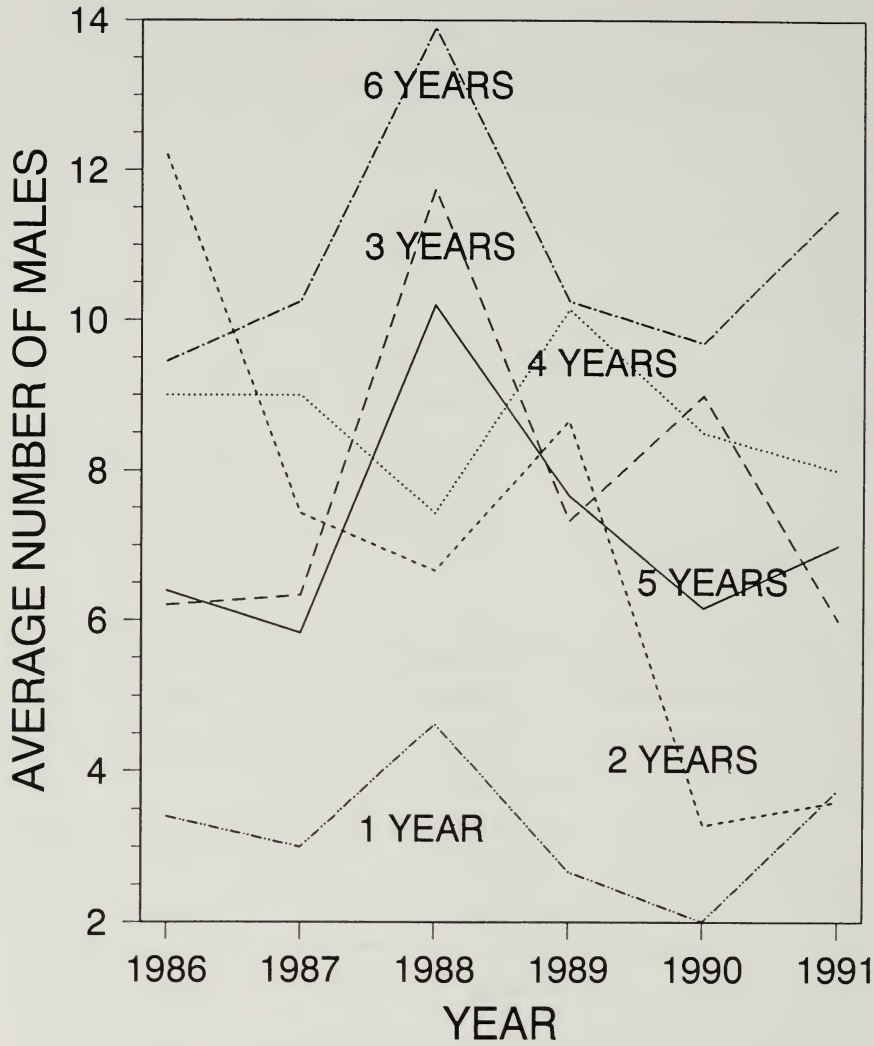

FIG. 2. Attendance of male Greater Prairie-Chickens at leks in northeastern Colorado, 1986–1991, in relation to the lek's stability (active for 1 to 6 years).

observations during normal display periods ($\bar{x}$ = 20.5 observations/bird [SD = 11.5, range 9–37]) were on leks an average of 94.5% (range 86.7–100%) of the time (each bird weighted equally). There was no correlation between number of observations/bird and the frequency of occurrence of males at leks ($r = 0.079$, $P = 0.797$). Although five males captured during

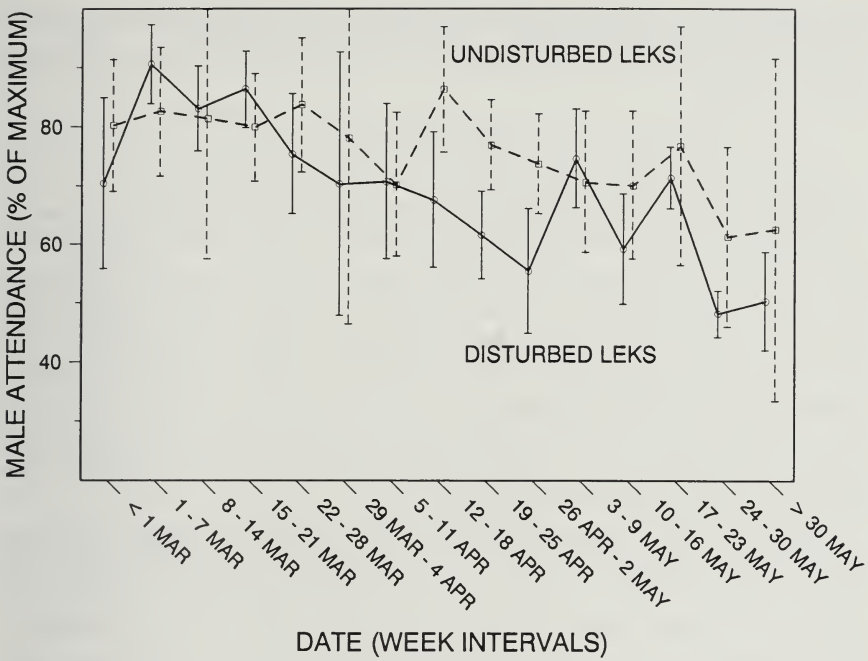

FIG. 3. Average weekly attendance (% of maximum attendance) of male Greater Prairie-Chickens on 28 undisturbed (not used for trapping) and 12 disturbed (used for trapping) leks on a 301-km² study area in northeastern Colorado, 1986–1991. Only leks with >2 counts within a breeding season were used in the analysis.

winter had slightly higher lek attendance rates than eight males captured on leks ($\bar{x}$ = 96.8 vs 93.1%), differences in rates of lek attendance by individual males were not detected (χ^2 = 10.647, df = 12, P = 0.559).

When lek attendance of radio-marked males was examined independent of individual differences, the frequency of occurrence of males at leks was 95.1% for 286 observations of 21 males (including eight males with less than 9 observations). Males captured during winter had slightly higher (χ^2 = 2.719, P = 0.099) frequencies of occurrence on leks than males captured on leks (96.9% vs 92.7%).

Although there were no apparent differences in lek visitation associated with age (t = 0.910, P = 0.382), yearlings visited more leks during the breeding season than adults. Three of four yearling males visited more than one lek, while only one of 17 adults visited more than one lek (χ^2 = 10.032, P = 0.002). In addition, one yearling was observed on four leks, while another was observed on six leks. The latter male also was

observed on two leks in the same morning. In only one case was a radio-marked yearling male not observed on a lek during the normal morning display period.

DISCUSSION

Leks differ with respect to stability, and permanent leks may be more desirable for territory acquisition than temporary leks. For example, Lewis and Zwickel (1980, 1981) determined that non-territorial yearling male Blue Grouse (*Dendragapus obscurus*) spent more time near permanent territories. Although there was no specific evidence of age composition of male Greater Prairie-Chickens at temporary leks, it was possible they were generally comprised of males unable to obtain territories on permanent leks (Cannon and Knopf 1981). Presumably these birds were more likely to be yearlings. Older males were more likely than young males to occupy territories on leks in Kansas (Robel 1970, Robel et al. 1970, Ballard and Robel 1974, Robel and Ballard 1974).

Yearling Greater Prairie-Chickens were observed visiting more leks than adults (at least six leks by one yearling male). Although multiple lek visitations have been reported in other populations, ages of males were rarely known (Silvy 1968, Arthaud 1970, Robel et al. 1970, Hamerstrom and Hamerstrom 1973, Robel and Ballard 1974). Removal of dominant males increased male-male interactions/morning/bird from 4.5 to 11.0, perhaps because of an influx of lower-status males (usually younger birds) onto vacant territories (Ballard and Robel 1974, Robel and Ballard 1974). Rippin and Boag (1974) found that removal of territorial male Sharp-tailed Grouse from leks resulted in an influx of new males; they suggested that newly established males were more likely yearlings that had previously been non-territorial in areas associated with the lek.

Movement of males among different leks, particularly young and/or non-territorial males, may explain why an average of about 80% of the maximum number of males were observed on leks during March and April (67% for leks active one to three years and 83% for leks active more than three years). Consequently, as the number of counts of males on a lek increases, the maximum number of males counted is also likely to increase. Although this consideration probably did not influence the results of this study (survey intensity was similar in each year), this consideration should be addressed in all studies.

There are numerous possible explanations for variability in stability of leks including (1) formation of smaller temporary leks near larger permanent leks, (2) differences in recruitment rates of males at permanent and temporary leks, (3) local and regional fluctuations in abundance of males, (4) compensatory changes in abundance of males at neighboring

leks (if one lek increases, an adjacent lek may decline), (5) movement of leks, (6) habitat changes, and/or (7) changes in location of nesting habitat for females.

Correlations in annual changes of male attendance at neighboring leks appeared to be either non-significant or negative, indicating that fluctuations in lek visitation may be caused by local, rather than regional, changes or "shifts" in abundance of males. These results were supported by anecdotal observations of shifts in actual lek locations. For example, in 1987 fire burned an area 0.5 km from one lek that was active for at least four preceding years (1984–1987). In the first spring following the fire (1988), several males were displaying on a new lek site within the boundaries of the burned area, while a few males remained on the old lek site. Only the new "burned" site was used in 1989–1991. In another example, a new lek formed on a newly disturbed site in 1990; the new lek was in the middle of, and relatively close to, three lek sites that had been occupied continuously since 1984 (in one case, the lek site was occupied as early as about 1910). The average combined attendance at the three "old" leks was 18 during 1986–1989, four in 1990, and zero in 1991; the new lek had 14 males in 1990 and 18 in 1991.

Several researchers have suggested there is a relationship between location of nesting habitat and lek locations; each lek may have its own population of females that breed at, and subsequently nest near, the lek (Westemeier 1972, Sanderson et al. 1973). Consequently, permanent leks may be in areas with 'better' nesting habitat. However, nests tended to be farther from the nearest lek than random locations in Colorado; distances between nests and the nearest lek were 0.23–2.39 km ($\bar{x}$ = 1.01 km) for 81 nests (Schroeder 1991). In addition, there was a positive correlation between number of males/lek and nest-lek distance ($r = 0.320$, $P = 0.001$).

Variation in lek attendance may be due to time of year (Bradbury et al. 1989), weather (Hamerstrom and Hamerstrom 1973), or overall status of the population. Visitation rates of Sage Grouse were > 90% during the period of peak male attendance at leks and between 67% (yearlings) and 100% (adults) during the peak of hen attendance (Emmons and Braun 1984). We found that lek visitation by Greater Prairie-Chickens in northeastern Colorado remained relatively constant at 95% throughout March and April.

Although northeastern Colorado is on the western edge of the Greater Prairie-Chicken distribution in North America, comparison of this population with those in other regions indicates they are comparable with respect to both density of leks and number of males/lek (Kansas [Horak 1985], Missouri [Christisen 1985], Nebraska [Kobriger 1965], North Da-

kota [Kobriger et al. 1988], and Wisconsin [Hamerstrom and Hamerstrom 1973]). Furthermore, brief lek searches on a 631-km^2 area surrounding the main 301-km^2 study area in northeastern Colorado during May 1988 resulted in detection of an additional 40 display sites. The abundance of leks in areas adjacent to the area intensively studied in northeastern Colorado indicates that this population was not on the "edge" of occupied range.

These results for male lek attendance pertain to serious issues concerning estimates of population size of Greater Prairie-Chickens and other prairie grouse. Counts of males are frequently used to estimate trend and size of populations of prairie grouse. Robel's (1970) paper has been cited as evidence that the actual number of males may be twice as high as the number counted on leks (Hoag and Braun 1990, Van Sant and Braun 1990). However, the data in this study indicated that most males (about 95%), may be attending leks every day. Thus, population size could be over-estimated if lek attendance rates of 50% are used.

In addition to lek visitation, methods of surveying lek attendance of prairie grouse should be evaluated. Accurate counts of males may be easier to obtain when birds are flushed than when observed from a distance. Some males may be on the edge of leks and, hence, difficult to observe. Additionally, permanent leks may be more consistent with respect to male attendance than temporary leks. Differences in attendance may be important if permanent leks are easier to find than temporary leks. This latter consideration could affect estimates of both lek density and male attendance (Cannon and Knopf 1981). The methodology for estimating numbers of males could be of critical importance if counts of males are used to estimate population size. Counts of male Greater Prairie-Chickens should be made only during the 1 March–30 April interval and preferably during the peak of hen visitation if estimates of male population size are desired.

If lek densities and/or counts of males are to be used for monitoring the status of populations, their respective disadvantages and advantages should be addressed. Although lek densities have been suggested to provide a better indication of a population's status (Cannon and Knopf 1981), lek densities may be difficult to estimate accurately. For example, conclusions might vary dramatically if some leks are not found. Similarly, estimates of lek numbers are rarely if ever obtained with a corresponding estimate of precision. Hence, the validity of the lek numbers is difficult to support. In contrast to lek density, numbers of males may be relatively easy to obtain and justify with estimates of precision. Although Cannon and Knopf (1981) suggested that numbers of males were not as accurate as counts of leks for evaluating the status of populations, understanding

the differences in male attendance associated with the stability of the leks may help improve the prospects for using counts of males.

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REPRODUCTION OF THE RED-COCKADED WOODPECKER IN CENTRAL FLORIDA

ROY S. DELOTELLE[1] AND ROBERT J. EPTING[2]

ABSTRACT.—Red-cockaded Woodpeckers (*Picoides borealis*) near the southern extreme of the species' range had a low fledging rate, high fledgling survivorship, and high level of breeder experience and adult survivorship compared to other populations. Breeding male and female survivorship was 10% and 23% higher, respectively, than northern populations. Tenure of helpers was higher than other populations, apparently as a result of high adult survivorship. The frequency of female helpers was higher (30%) than reported for other populations (5%). Group size ranged from two to five members and averaged 2.4 birds prior to nesting. Reproduction in central Florida was lower than other populations (1.0 vs 1.6 fledglings per group). Experienced pairs without a helper produced significantly more fledglings than experienced pairs with a helper (1.45 and 0.87 fledglings/group, respectively). Reproductive success was correlated with breeder experience, outside intrusion rate, and territory size. *Received 27 June 1990, accepted 1 Nov. 1991.*

Red-cockaded Woodpeckers (*Picoides borealis*) breed cooperatively in groups of two to six adults. One breeding pair within each group lays a single clutch (Ligon 1981, Lennartz et al. 1987, Walters et al. 1988). Breeding success probably is affected by the level of disruption due to the intrusion of alien Red-cockaded Woodpeckers, as well as age and breeding experience and possibly habitat quality (Ligon 1981, Lennartz et al. 1987). In central Florida, territories are larger with very little extra-territorial habitat. In northern populations, territories are smaller with substantially more extra-territorial habitat (Hooper et al. 1982, Repasky 1984, Blue 1985, Porter and Labisky 1986, DeLotelle et al. 1987).

Habitat differences between populations could affect demographics, social dynamics, and reproductive success. We examined the effect of such differences in the present study in order to (1) document demography and social dynamics in this population, (2) develop a model of the influence of social and habitat factors on reproductive success, and (3) compare demography and social dynamics between populations.

METHODS

The 1328-ha study area, the Curtis H. Stanton Energy Center, is 21 km southeast of Orlando, Florida. The habitat was dominated by longleaf pine (*Pinus palustris*) with an understory of saw palmetto (*Serenoa repens*) (<1 m) and very few hardwoods, interspersed cypress domes, bayheads, and wet prairies (DeLotelle et al. 1983, DeLotelle et al. 1987).

[1] Alvarez, Lehman & Associates, Inc., 2444 N.E. 1st Blvd., Suite 500, Gainesville, Florida 32609.
[2] Dept. of Resource Management, St. Johns River Water Management District, P.O. Box 1429, Palatka, Florida 32178.

Pine habitat occurred in distinct stands of varying ages and densities. Pine tree characteristics were based on aerial photographs and 25 field-inspected plots for dbh, density, age, and basal area.

The study area was searched annually for nesting and roosting trees. Eleven Red-cockaded Woodpecker groups were studied from the late summer of 1980 through the fall of 1987. These 11 groups were part of a larger population of an additional 26 groups in similar pine habitat surrounding the study area. Birds were captured by placing mist netting on a wire frame over the entrance to roost cavities during mornings and evenings and banded with color-coded plastic leg bands and U.S. Fish and Wildlife Service identification bands. The banding frequencies for all group members during the post-fledging and fall/winter observation periods were 83% (N = 120 bird-years) and 96% (N = 128 bird-years), respectively. During nesting, 95% (N = 85 bird-years) of group members were banded. Roost trees for individuals (N = 131) were determined during banding activities, territorial monitoring studies (N = 95 days), and seasonal censusing (N = 16 days). Cavity tree locations for each group were plotted on aerial photographs (1:4800) and the location of roosting birds recorded. During the post-fledging periods all unbanded birds in the group counts were fledglings. For the two years of no reproductive observations (1983 and 1986), two additional summer censuses, including banding activities, were conducted to establish group composition.

Each group was monitored during the four seasons (winter and spring only in 1985) for composition, breeder replacement, and intruder frequency. The reproductive survey included a 1–3 h weekly census of each group to determine composition and participation of individuals in nesting activities. Group composition was determined by observing band combinations on individual birds during daily foraging trips (N = 215 days), nesting activity (N = 69 days), and other behavioral censuses (N = 30 days). Sampling usually began as the birds started their daily activity and included a record of observation time. Both the behavior of new birds interacting with residents of a territory and the behavior of group members during interactions with neighboring groups were recorded during 1909 h of observation.

Individual males and females were assigned breeding status if they were present as a pair only on the territory. For the other groups with helper males, breeding status was assigned to the male in whose roost tree nesting occurred (N = 27) (see Walters 1990). For one group with a female helper, copulation was observed between the breeding male and the female that was assigned breeding status. In the other group with a female helper, breeding status was assigned to the female that appeared to dominate the other female at foraging sites. Subsequently, breeding status was assigned to males and females that had previously resided on a territory as breeders. Of the 35 group-years, the breeding status of 24 of the male bird-years and 31 of the female bird-years was assigned by virtue of being the only male or female present in the group. Breeding status was also verified based on observed copulations (N = 5 pairs). Five of the helpers were banded as fledglings on their natal territory. Survival and turnover frequencies for seven years were calculated by comparing the censuses of banded birds tabulated from one year to the next.

Intruder status, which included helpers, displaced breeders, floaters, and birds of unknown status, was assigned to any Red-cockaded Woodpecker observed on a territory in which it was not a member of the resident group. Helper status was assigned to birds, other than breeders, occurring on territories for more than one year that had little or no overt agonistic interaction with other group members and participated in nesting activities and inter-group territorial interactions. Displaced breeders were known breeders that were subsequently observed in other territories after their replacement. Floaters were banded birds with no observed previous breeding history that were observed on two or more territories in a survey year and were not regularly associated with any single group. Floaters were followed from their roost cavities on seven occasions. The behavioral interactions between residents and intruders were later standardized to an 11.5-h sampling day.

Thirty-five group years of reproductive observations were compiled. Visual inspections of nest trees were made weekly during April and May and more frequently thereafter depending on nestling development. During 1981, fledging rates were determined by counting group members weekly during nesting and recounting group members and fledglings during the fledging process. Based on behavior, all fledgling censuses during 1981 were conducted within one to three days of fledging (Jerauld et al. 1983). Thereafter (1982, 1984, 1985, 1987), cavity contents of nest trees were recorded weekly or more often during April through July with the aid of a mirror and a flashlight. Ninety-three cavities were inspected for occupancy by other wildlife species, including 60% and 95% of completed cavities for 1985 and 1987, respectively. Feeding rates for individual adults were compiled throughout the day for nests of 10-day and older nestlings and for fledglings.

Annual territory sizes were measured in 1981–1984 (N = 6 territories) and 1986–1987 (two previous territories and five previously un-sampled territories). Movements of groups were recorded at five minute intervals on photocopies of aerial photographs (scale 1:4800) for a total of 1647 h following methods described by DeLotelle et al. (1987). Groups were generally followed from the morning to well into the late afternoon. On occasion, groups were followed all day or from noon until roosting (23 of 215 days). Territory size and configuration were based on a modified minimum polygon procedure, connecting points of territorial interaction and areas of repeated use where no interactions were observed (Hooper et al. 1982). Territories not measured (7 of 35 group-years) were estimated from figure 1 of DeLotelle et al. (1987). Nesting home ranges, based on an additional 146 h of observing daily foraging, were determined for six territories during the nestling stage. Areas for those nesting home ranges not measured were taken to be a 46.5-ha circle around the nest tree.

A multiple regression model (SAS Institute 1985) was constructed of reproductive success versus breeder experience, group size, habitat quality index, annual territory size, and intrusion rate. Breeding success categories were no eggs laid (1), eggs laid but not hatched (eggs only) (2), one successful fledgling (3), and two or more successful fledglings (4) (van Riper 1984). Breeder experience levels were: no previous experience, one member with experience, and both members experienced (Lennartz et al. 1987). Group size was either a breeding pair without a helper or a pair with one (male or female) helper. The habitat quality of the nesting home range was evaluated by mean age and density of pine for the territories of each group-year (Equation 1, DeLotelle et al. 1987). Habitat quality influences group size (Brown and Balda 1977), and foraging habitat preference as a quality index has been used in other Red-cockaded Woodpecker studies (Lennartz et al. 1987). Intruder rates were standardized to a field effort of an 11.5-h day. The number of intrusions for each group-year was divided by the standardized sampling effort.

RESULTS

Group composition and survivorship.—Red-cockaded Woodpecker groups consisted of two to five individuals. There were 20 group-years (57%) for pairs without a helper and 15 (43%) for pairs with a helper. Group size (N = 35 group-years) prior to the nesting season was 2.4 ± 0.5 (SD) birds and increased to 3.4 ± 0.9 after nesting to include 29% fledglings. The mean group size during the winter was 3.1 ± 0.8 birds (N = 41 group-years) and consisted of 65% breeders, 25% non-adults and 10% helpers with more than one year of experience. Females comprised 30% of the helpers and were present during the first four study years, but not the latter three years.

Annual retention of individual breeders on resident territories was 84% ± 18 (N = 48) and 81% ± 21 (N = 48) for males and females, respectively. Survivorship in the study area for breeding males and females was 90% and 93%, respectively, assuming birds that disappeared from the study area died. Helpers continued in that status on their resident territories for a mean duration of at least 2.2 ± 0.7 years (N = 10) (2.0 years for females and 2.3 years for males). Based on the non-adult component of the mean post-fledging and mid-winter group size (1.0 and 0.73 birds, respectively), the seven-month juvenile survivorship in the population was 73%.

Territorial interactions and intrusion.—Breeders and male and female helpers were observed participating in inter-group conflicts and expulsion of intruding groups. Interactions between residents and non-residents occurred as a result of the inter-territorial movements of helpers, male and female floaters, and displaced breeders (Table 1). The 0.7 ± 0.3 intrusions per day by these birds were in addition to the 0.5 ± 0.3 inter-group conflicts per territory-day. While female floaters accounted for 4% of the population during nesting and 9% during winter, they were observed in every territory and their movements accounted for 27% of the intrusions. About one-third of female floater intrusions resulted in little response from residents while about one-third were aggressively expelled and involved interaction with the breeding pair. Female floaters and other alien birds were observed to roost (N = 6) and forage in territories while remaining un-associated with the resident group.

Helper males and helper females accounted for 11% of all intrusions into surrounding territories (Table 1). On five occasions, a helper male foraged on a neighboring territory in association with a female floater, and on one occasion with a helper female on her territory. Two female helpers which had been in that status for two and three years, respectively, were observed in several territories before displacing a breeding female. Helper males and females, however, were consistently observed foraging with their resident group with little or no overt negative interactions with the resident breeders and participated in inter-group territorial interactions.

Displaced breeders accounted for 9% of all intrusions. The majority of displaced breeding females were observed foraging in loose association with resident groups. Four displaced breeders, however, eventually attained breeding status, three outside of the study area. In a one year period, a chain of displaced and replaced breeding females occurred on three different territories in succession.

Prolonged and persistent interaction between one member of a breeding pair and an intruder was observed on four territories. The conflicts consisted of aerial chases and displacements on trees between the alien bird

TABLE 1

FREQUENCY OF GROUP/INTRUDER BEHAVIORS BY INTRUDER STATUS DURING TERRITORY AND NEST MONITORING FOR 11 GROUPS (M = MALE; F = FEMALE)

Behavior	Intruder status										
	Helper		Floater		Breeder		Displaced breeder				
	M	F	M	F	M	F	M	F	Unknown[a]	Total	Rate[b]
Loose association	2	1	5	14	—	1	1	8	26	58	0.35
Foraging[d]	6	1	—	5	—	—	—	—	—	12	0.08
Interactions	1	2	—	3	—	—	—	2	11	19	0.11
Intruder expulsion	—	—	—	9	—	1	—	—	17	27	0.16
Total	9	4	5	31	0	2	1	10	54	116	0.70
Breeder[c] replacement	1	2	—	2	—	—	1	3	7	16	

[a] Unbanded, or color bands not observed.
[b] Number of intruders per 11.5-h day.
[c] Three of these breeder replacements occurred outside study area.
[d] Helper and floater foraging together.

and a specific breeder. In two cases the group included a helper although the intruder was of the opposite sex. The helper and other breeder had little involvement in the interactions. Two of the displaced breeders (a male and a female) were later observed as breeders on other territories. Competition involving aerial chases and spiral chases on trees was also observed between a displaced breeding female and a former female helper (from another group) for a third female's breeding position.

Nesting and helping behavior.—Clutch size averaged 2.9 ± 0.8 eggs, with a mean laying date of May 13 ± 17 days, and was significantly (t = 5.4, $P < 0.001$) larger for experienced (3.3 ± 0.4 eggs, N = 12) than for inexperienced (1.8 ± 0.5 eggs, N = 4) females. Egg incubation was performed by all group members. Nesting home ranges averaged 46.5 ± 23.7 ha (N = 6) and contained a mean of 4237 ± 2293 pine stems, with a mean age of 72 ± 20.6 years and a mean dbh of 20.3 ± 2.6 cm.

Both parents fed nestlings, males accounting for 56% and females 44% of trips to the nest (N = 903). Female helpers were often observed feeding nestlings and fledglings, but no frequency data were collected relative to that. Fledgling feeding through September was 7.8 visits/h, declining in October to 2.0 visits/h. During June, fledgling (five male and one female) feeding was performed primarily (94%, N = 534 feedings) by the breeding male. One-year-old helpers were not observed feeding fledglings during the first month after fledging. While foraging, the one-year-old helper (three males and one female) reacted negatively when approached on a tree by the fledgling, often resulting in extended flight movements and vocalization by all group members. By mid-August, one-year-old helpers accounted for 19% of feeding visits to fledglings. Second-year and older helpers commenced feeding fledglings shortly after the young fledged.

Breeding success.—Eggs were laid in 31 (89%) of the 35 group-years. Nestlings were observed in 26 (84%) of these 31 nesting group-years. Of these 35 group-years, only eight included the same group structure as in previous years due to breeder turnover and the presence or absence of helpers. For pairs without a helper, 43% (N = 3) of the unsuccessful nests were egg failures while 57% (N = 4) were no nesting attempt. For pairs with helpers, all nest losses (N = 2) were egg failures. Four of the five nest failures occurred in groups with one or both breeders inexperienced. No competitors or predators were observed in or near the nest cavities at the time of egg loss, and breeding males were observed roosting in the nest cavities one to seven days later. In addition, 93 cavity inspections for predators and competitors revealed that 6% were occupied by other bird species, including Red-bellied Woodpeckers (*Melanerpes carolinus,* 3%), Eastern Bluebirds (*Sialia sialis,* 2%), and un-identified nestlings (1%). Wasps were found in 7% of the cavities.

TABLE 2
REGRESSION COEFFICIENTS OF BREEDING SUCCESS VERSUS MEAN BREEDER EXPERIENCE, HABITAT QUALITY INDEX, GROUP SIZE, TERRITORY SIZE, AND LEVEL OF INTRUSION

Parameter	Coefficient ± SE	*P*
Intercept	−1.359 ± 0.876	
Experience	1.586 ± 0.293	<0.001
Habitat quality	0.041 ± 0.023	0.086
Group size	−0.069 ± 0.212	0.749
Territory size	0.015 ± 0.005	0.008
Intrusion	−2.325 ± 0.734	0.005

The fledging rate per group was 1.0 ± 0.8 (N = 35 group-years). Successful nesting by pairs without a helper (1.54 ± 0.69, N = 13) produced significantly ($t = 2.21$, df = 25, $P = 0.039$) more fledglings than pairs with helpers (1.08 ± 0.29, N = 13). Fledging rates were similar among groups whether they had a male or female helper. In the cases where both breeders were experienced, pairs without a helper produced significantly ($t = 2.12$, $P = 0.046$) more fledglings (1.45 ± 0.82, N = 11) than pairs with a helper (0.87 ± 0.33, N = 8). This result is more striking since the mean experience-years of male and female breeders for 1984 and later years, an index to age, was slightly higher for pairs with a helper (3.8 and 2.7 years, N = 6) than for pairs without a helper (3.4 and 2.6 years, N = 7). Additionally, three groups composed of the same experienced male had mean fledging rates of 0.75 with and 1.4 without a helper in different years.

The level of reproductive success (no eggs, eggs only, one fledgling, and two or more fledglings) was correlated significantly ($R^2 = 0.76$, $P < 0.0001$, N = 25) with breeder experience, intrusion rate, and territory size (Table 2). The magnitude of the regression slopes suggests that reproductive success is most responsive to level of intrusion and secondarily to breeder experience.

DISCUSSION

Demographic characteristics of the central Florida population include high level of breeder experience, high adult survivorship, high frequency of successful nests, low fledging rate, and high fledgling survivorship as compared to other populations (Lennartz et al. 1987, La Branche 1988, Lennartz and Heckel 1988, Walters et al. 1988). Annual retention of male and female breeders on resident territories (84 and 81%, respectively) is higher than in North Carolina (73 and 56%), South Carolina (78 and

68%), and Georgia (72 and 51%) populations (Lennartz and Heckel 1988, Walters et al. 1988). The percentage of successful nests in central Florida (84%) appears lower than in South Carolina (93%) but higher than in either the Georgia (69%) or North Carolina (72%) populations. In sharp contrast to results from other populations, central Florida groups with helpers fledged nearly one bird less per group than either the South Carolina or North Carolina populations (0.9 vs 2.05 and 1.99, respectively). Groups without helpers produced only 0.4 fewer fledglings than the northern populations (1.4 South Carolina and 1.38 North Carolina, respectively). The overall differences in breeding success between central Florida and northern populations (1.0 and 1.6 fledglings/group, respectively) would be expected to be much smaller given the high experience level of breeders and reduced nest competition from other species in central Florida.

Social structure and behavior.—The proportion of groups with helpers was 43% compared to 46% and 30% for South Carolina and North Carolina, respectively. Female floaters accounted for 4% to 9% of the population compared to an apparently smaller percentage in North Carolina. Group social structure was similar to other populations but included a greater percentage of female helpers.

A higher frequency of intrusion by females searching for breeding vacancies should occur because of the different dispersal strategies employed by male and female Red-cockaded Woodpeckers (Walters et al. 1988). Female floaters accounted for 50%, and other female classifications for 26%, of banded bird intrusions within territories (Table 1). The frequency of interactions generated by the movement of these birds through neighboring territories and other inter-group interactions appear to be substantially higher in central Florida (1.2 and 0.8 conflicts/day, respectively) than for North Carolina (Repasky 1984, Blue 1985). The replacement and subsequent movement of female breeders appeared to be the result of competition more often in central Florida than in North Carolina, where most such movements follow loss of the mate (Walters et al. 1988).

Demographics and social structure.—Given the relatively low reproductive rate in central Florida, it might be expected that the frequency of helpers would be lower than in other populations. In central Florida, helper tenure for males is higher (2.2 vs 1.6 years, respectively) than in other populations (Fig. 3.9, Walters 1990). The dispersal options of young birds may be reduced in central Florida because of reduced availability of breeding positions (Fig. 3.2, Brown 1987). A 30% female helper frequency in central Florida compared to 5% in both South Carolina and North Carolina, where turnover rates of adult females are greater, further supports the hypothesis of social dynamics being altered by adult survivorship. Dispersing females, with breeding positions scarce, are more

likely to end up as floaters or remain on the natal territory. Those females that do disperse and attain breeding status are more likely to do so through aggressive interaction with an established breeder.

It is noteworthy that in central Florida, experienced pairs with a helper produced significantly ($P < 0.05$) fewer fledglings than experienced pairs without a helper (0.87 and 1.45, respectively). A similar negative or non-positive effect of group size on reproduction has been reported for the Jungle Babbler (*Turdoides striatus*) and Green Woodhoopoe (*Phoeniculus purpureus*) (Gaston 1978, Ligon 1981). Pairs with a helper should have produced significantly more fledglings given the relatively high experience level of the breeding pair. There may be some negative interaction occurring between the pair and the helper that is more pronounced in low pine stocking habitat. Interference and competition involving breeder-helper conflicts occur in other cooperative breeders and may not involve overt aggression (Zahavi 1974, Emlen 1982, Mumme et al. 1983, Hannon et al. 1985).

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THE INFLUENCE OF HABITAT VARIABLES ON MARSH BIRD COMMUNITIES OF THE CONNECTICUT RIVER ESTUARY

ROBERT J. CRAIG[1] AND KATHLEEN G. BEAL[2]

ABSTRACT.—Between 1974 and 1987, we studied summering birds of estuarine marshes along the Connecticut River in Connecticut in order to seek generalizations concerning the principal habitat features associated with species richness and species composition. Features of habitats investigated were (1) area, (2) environmental heterogeneity, (3) isolation, (4) water cover, (5) mudflat cover and, indirectly, (6) tidal and water salinity regimes. We also explored the value of large vs several small habitats in preserving marsh bird communities. Species inhabiting the marshes were divided into breeders (species that nested in marshes) and users (species that used marshes or associated creeks and flats primarily for feeding). Breeder species richness showed a significant positive relationship to marsh area and showed a negative relationship to water cover and environmental heterogeneity. User richness, in contrast, was positively related to proximity of additional marsh habitat (a measure of isolation), water cover, and environmental heterogeneity. Clustering pairwise comparisons of marshes showed that saline, strongly tidal marshes differed from freshwater, weakly tidal marshes. However, species composition was likely a consequence of the entire suite of differences which distinguish saline and freshwater marshes. Separately analyzing data on regularly occurring species, as opposed to all species recorded during the study period, produced similar results. Hence, the longer term view gained by considering all potentially occurring species yielded little additional information about habitat factors influencing species richness. In contrast, separately analyzing data on breeders and users demonstrated that these species groups had divergent principal habitat requirements. Series of small marshes proved to be equivalent or superior to a large marsh in supporting species richness. However, species occurring infrequently along the Connecticut River predominated at large marshes.
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Evaluating the influence of habitat variables on bird species has been important for understanding patterns of avian community structure (Terborgh 1971, 1985; Anderson and Shugart 1974) and, consequently, for avian community management (Kantrud and Stewart 1984, Wiens and Rotenberry 1985). However, dissecting community-habitat relationships among the diverse avifaunas of structurally complex systems like three-dimensional forests may be difficult. Herbaceous marshes, although still complex, are essentially two-dimensional environments that support relatively few bird species. In ecological investigations, this relative simplicity is advantageous because the role of habitat variables in influencing

[1] Dept. Natural Resources Management and Engineering, U-87, Univ. Connecticut, Storrs, Connecticut 06269-4087. Present address: Northern Marianas College, P.O. Box 1250, Commonwealth No. Mariana Islands, Saipan, MP 96950.
[2] Dept. Mathematics and Statistics, Wright State Univ., Dayton, Ohio 45435.

community parameters may be less difficult to identify. We therefore studied birds of estuarine marshes along the Connecticut River in Connecticut in order to seek generalizations concerning avian community-habitat relationships. We wished to determine the principal habitat features associated with species richness and species distribution along the estuary. Furthermore, we investigated specific habitat features of estuarine wetlands likely to affect birds of these systems.

Habitat factors known to influence bird species richness and distributions in marshes are similar to those influencing terrestrial communities and include (1) tract size (Brown and Dinsmore 1986), (2) habitat diversity (Weller and Spatcher 1965, Weller and Fredrickson 1973, Kantrud and Stewart 1984), (3) isolation (Brown and Dinsmore 1986), and (4) history, including human impacts (Cottam and Bourne 1952, Clarke et al. 1984). Other habitat-related factors that affect marsh birds include water cover (Weller and Spatcher 1965), water level (Jackson 1983), tides (Burger 1985, Swift, 1988), and water salinity (Poulson 1969). We chose to study the relationship of marsh bird populations to (1) area, (2) environmental heterogeneity, (3) isolation, (4) water cover, (5) mudflat cover, and indirectly, (6) tidal and water salinity regimes. Historic changes in this system's avifauna are also reviewed.

Because marshes often exist as islands of discrete habitat, their bird communities have been studied in light of island biogeographic theory (e.g., Brown and Dinsmore 1986). Using predictions generated by this theory, investigators (e.g., Brown 1971, Butcher et al. 1981) have attempted to infer optimal designs for wildlife refuges. However, widely divergent viewpoints on the value of single large vs series of small refuges have been promoted (Simberloff and Abele 1976, Cole 1981). Furthermore, continental bird communities potentially differ from oceanic islands in the importance of such phenomena as colonization, extinction, and species use of surrounding habitats (Blake 1983). In temperate marshes, most residents are long-distance migrants with high dispersal ability. Moreover, the surrounding uplands can be used by many marsh species, whereas the open ocean is unsuitable habitat for terrestrial birds. With these considerations in mind, we explore the value of a large vs several small habitats in preserving marsh bird communities.

Earlier investigations of birds of the Connecticut River include Clark (1897), who described the nest of the Black Rail (*Laterallus jamaicensis*), Billard (1948), who estimated population densities of rails in freshwater marshes, and Poulson (1969), who studied the physiology of the Seaside (*Ammodramus maritima*) and Sharp-tailed sparrows (*A. caudacuta*). Several workers (e.g., Spitzer and Poole 1980) have studied population declines in nesting Ospreys (*Pandion haliaetus*) brought about by pollution of the river with toxic chemicals.

TABLE 1
SUMMARY OF HABITAT FEATURES OF THE CONNECTICUT RIVER MARSHES

Site	Type	Tides	Water salinity	Distance from river mouth (km)
Great Island (GI)[a]	salt marsh	yes	high	0.1
Black Hall River (BH)	salt marsh	yes	high	0.8
Upper Island (UI)	transitional	yes	moderate	1.3
Ragged Rock Creek (RR)	transitional	yes	moderate	2.6
Ayer's Point (AP)	brackish	yes	low	5.4
Lord's Cove (LC)	brackish	yes	low	6.0
Whalebone Creek (WC)	freshwater	yes	none	17.5
Pecausett Meadows (PM)	freshwater	yes	none	40.0
Cromwell Meadows (CM)	freshwater	yes	none	42.5
Dead Man's Swamp (DM)	freshwater	no	none	45.0
Wethersfield Meadows (WE)	freshwater	no	none	52.0

[a] Abbreviations of marsh names used in subsequent tables in parentheses.

STUDY AREAS AND METHODS

Study areas.—The Connecticut River estuary is bordered by a series of marshes totaling about 1200 ha. The 11 marshes studied intensively range from tidal salt marshes near the river mouth to nontidal freshwater marshes 52 km upriver (Table 1). Tidal amplitude, which during low river flows averages 1.1 m at the river mouth, declines to 0.5 m 60 km north at Hartford (NOAA 1983). Maximum water salinity varies from 17 ppt near the river mouth to 0 ppt 23 km upriver (Meade 1966).

A vegetation gradient is related to gradients in tidal amplitude and salinity. Five principal associations occur that are each structurally distinct because the diversity of dominant species is low. Around the river mouth are (1) shortgrass salt meadows composed largely of *Spartina patens, Distichlis spicata,* and *Juncus gerardi,* only occasionally inundated by tides (high salt marsh), and (2) rank intertidal cordgrass marshes of *Spartina alterniflora* and *Scirpus robustus* (low salt marsh). At about 2.6 km upriver, salt meadows are invaded by (3) strong-stemmed cattail-reed (*Typha angustifolia, Phragmites australis,* respectively) patches, which by 6.5 km upriver almost completely dominate the marshes. By 14 km upriver, freshwater communities occur, particularly (4) relatively soft-stemmed bulrush-tuckahoe-horsetail (*Scirpus fluviatilis, Peltandra virginica, Equisetum fluviatile,* respectively) marshes, and (5) floating-leaved pickerelweed-bullhead lily (*Pontederia cordata, Nuphar variegatum,* respectively) associations.

Habitat measurements.—Principal study sites (Table 1) included replicates of each of the four principal marsh types of the estuary: (1) salt marshes, containing predominantly high and low salt marsh; (2) transitional marshes, containing high and low salt marsh and cattail-reed habitats; (3) brackish cattail marshes, containing cattail-reed and low salt marsh; and (4) freshwater marshes, containing softstem bulrush and floating-leaved habitats. To assess further the effects of habitat size on species composition, we also studied separately the five freshwater marshes, including a large marsh and four relatively isolated, vegetationally similar small ones with a combined area similar to that of the large marsh.

We mapped vegetation types at each marsh on base maps made from 1:2400 aerial photographic enlargements. Marsh images from 1:12,000 1981 color infrared transparencies were superimposed on the enlargements with a Bausch and Lomb Zoom Transfer-scope.

Vegetation boundaries were then determined through photointerpretation (Civco et al. 1986). To check precision, maps were also field-checked for ground truth. We determined the area of each marsh and its component habitats by measuring the base maps with a compensating polar planimeter. Similar maps, based primarily on photointerpretation, were made for six of the largest marshes on 1:2400 1968 black-and-white photographic enlargements in order to assess the extent of vegetation change during the study period. Habitat patches covering <0.25 ha were too small to measure.

The area of water cover was determined on these same maps by measuring open water within the perimeter of each marsh. Although this was an imperfect measure because some marshes were bordered by the river while others were bordered by upland, we believe proximity to the river might be considered a constant because all sites were within 150 m of the main river channel. The extent of mudflats exposed at low tide was determined on the maps by measuring the mudflats within 100 m of the perimeter of each marsh. To determine the proximity of other marsh habitats, a measure of isolation, the distribution of all marshes of the Connecticut River was traced on acetate cellulose laid over 1:12,000 black-and-white photographs. The area of other marshes present within 1 km of the perimeter of each study site was then measured. Although the distances to which we measured mudflats and other marshes were arbitrarily chosen, this procedure included most mudflats and other marshes near the study sites. Finally, the area of each marsh was computed in two ways, considering (1) only vegetated areas (marsh area) and (2) vegetated areas, mudflats and water cover (total area).

Bird surveys.—Marsh bird distributions were studied by Craig from 1974 to 1987. Data on summering birds were gathered between early May and mid-July, but observations that shed additional light on breeding status were made at all seasons. Depending on the size of the marsh, 5–10 h per day were typically spent surveying, but shorter visits were made when checking for the presence of individual species. Observations usually began at dawn, and all sites were also visited from afternoon to dusk. Most sites also were visited after dark. Birds were observed for 1073 h, including 29–81 h of summer observations at each of the 11 principal study areas.

While crossing a marsh on foot or by boat during a visit, we recorded all bird species encountered. Data from all visits were used to prepare lists of summering species for each site. Based on our data and those of collaborating observers, species were divided into those that were (1) regular—occurring at a site most years, and (2) occasional—occurring irregularly, generally <50% of breeding seasons. This distinction permitted comparisons of habitat variables with the typical assemblage of birds (regular species) and with the entire potential assemblage of birds (regular + occasional species) that found suitable habitat conditions along the estuary. The latter comparison allowed for exploration of habitat relationships in the absence of such factors as externally driven population phenomena.

Summering species were classified into two additional groups: (1) breeders—species that spent their entire day on marshes, nesting there, and using marsh vegetation, creeks, or tidal flats, and (2) users—species that used marshes or associated creeks and flats primarily for feeding but which nested elsewhere. This distinction permitted separate analysis of habitat variables with species closely tied to marsh environments for all aspects of their survival and of species that opportunistically exploited marshes for food resources that were in many cases indefensible (e.g., schooling fish).

In most cases, breeding evidence was confirmed (nests, eggs, nestlings, fledglings, family groups) for those species termed breeders. However, we classified summering individuals of several species as breeders because in their habitat use they best conformed to this definition. For example, the few nonbreeding Northern Harriers (*Circus cyaneus*) present appeared to feed exclusively in marshes and at least attempted breeding. Similarly, Wood

Ducks (*Aix sponsa*) were called breeders because they spent essentially all their time in marshes even though they nested in tree holes or boxes adjacent to the marshes. We did not include postbreeding flocks (e.g., swallows, herons), migrants, or summer vagrant species in this study but focused solely on birds of the breeding season.

Analysis.—Shannon and Weaver's (1963) formula was used to compute indices of habitat diversity, H′ from the proportion of each habitat in a marsh. We made separate computations for marsh vegetation types (vegetation heterogeneity) and for vegetation, water, and mudflats considered together (habitat heterogeneity).

To compute habitat similarity between pairs of marshes we developed an index of similarity (IS) based on that of Spatz (Mueller-Dombois and Ellenberg 1974):

$$IS = \sum d_i n^{-1} / \sum (p_i + q_i) tot^{-1}$$

where d_i is the proportion of habitat i at a marsh divided by the larger proportion at the compared marsh, n is the total number of habitats at the two marshes, p_i and q_i are the areas of the shared habitat i at the compared marshes, and tot is the total area of all habitats at the compared sites. The numerator weights the index for the number of habitats and the denominator weights for proportionate similarity in cover. We used this formula to determine vegetation similarity and similarity of all habitats (habitat similarity).

To compute differences in marsh area, mudflat area, and marsh proximity, we developed the index of difference (ID): $ID = |a_i - a_j| / (a_i + a_j)$, where a is the area of cover at the compared marshes i and j. Similarity in species composition was assessed by dividing the number of shared species by the total species pool at the compared marshes.

Using diagnostics described by Myers (1986) and SAS (1985) Proc Reg procedures, we evaluated collinearity among the seven habitat regressor variables. We then analyzed species richness vs regressor variables from each set of independent variables to determine the best fitting statistical models. In making decisions concerning best fit, we considered the significance of the parameter estimates, r^2 (the coefficient of determination), collinearity diagnostics (correlations of estimates, variance inflation factors, eigenvalues, condition numbers, variance proportions), and residual plots. Normality assumptions were assessed with normal probability plots of residuals generated using the final regression model.

Relationships among marshes in their species and habitat similarities were explored with cluster analysis, a descriptive statistical technique (Morrison 1990) and SAS (1985) Proc Cluster procedures. Three clustering methods were performed: average linkage, complete linkage, and centroid hierarchical, with cluster number determined by the computer. Cluster analysis was chosen because similarity data were not independent, and conventional hypothesis testing was, therefore, not valid.

RESULTS

Habitat-species richness relationships.—Marsh area, total area, marsh proximity and mudflat cover (Table 2) all tended to increase toward the river mouth, and five measures of collinearity showed them to be highly related. Hence, they constituted a set of variables, one of which was included in each multiple regression model investigated. Although direct measurements were not made on tidal and salinity patterns, they appeared to correlate positively with these measures. Vegetation and habitat heterogeneity (Table 2) were also highly related to each other, although not to other habitat measures. They constituted another set of variables, one

TABLE 2
MEASUREMENTS OF HABITAT FEATURES AT 11 CONNECTICUT RIVER MARSHES

Site	GI	BH	UI	RR	AP	LC	WC	PM	CM	DM	WE
Heterogeneity											
Marsh	0.77	0.70	0.59	0.84	0.23	0.24	0.74	0.33	0.31	0.38	0.39
Habitat	0.97	1.22	1.11	1.11	0.63	0.78	1.30	0.91	0.84	0.42	0.42
Area (ha)											
Marsh	145.6	56.4	121.6	155.4	39.5	215.2	23.1	21.6	119.7	26.9	30.7
Habitat	153.4	74.7	155.2	169.5	44.9	274.3	31.6	30.3	146.6	27.1	30.9
Mudflats (ha)	3.6	13.6	24.1	6.7	1.1	6.6	3.1	0.6	7.4	0	0
Water (ha)	4.2	4.7	9.5	7.5	4.4	52.4	5.5	8.1	19.7	0.2	0.2
Proximity (ha)	131.0	161.3	188.2	49.5	31.0	76.6	5.6	10.4	6.4	1.2	12.9

of which was included in each multiple regression model tested. Water cover (Table 2) was independent of all other habitat measures and was, therefore, entered into all multiple regression models.

In comparing species richness to habitat variables, the model best fitting both all (Fig. 1a) and regular (Fig. 1b) breeders contained total area, water cover, and habitat heterogeneity (see Craig 1990 for a complete listing of species occurrence). All breeder richness was inversely related to water cover and habitat heterogeneity and directly related to total area. All three habitat measures made a significant contribution to the model ($r^2 = 0.94$; total area $t = 9.93$, $P < 0.0001$; water cover $t = -6.58$, $P < 0.0003$; habitat heterogeneity $t = -2.43$, $P < 0.05$; 7 df). Replacing habitat heterogeneity with vegetation heterogeneity only slightly reduced the fit of the model.

The relationship of regular breeder richness to water cover and total area was similar to that of all breeders, but the partial slope for habitat heterogeneity was not significant in the presence of the other two habitat measures ($r^2 = 0.87$; total area $t = 6.45$, $P < 0.0004$; water cover $t = -5.15$, $P < 0.0001$; habitat heterogeneity $t = -0.39$, $P < 0.70$; 7 df). Replacing total area with marsh area and/or habitat heterogeneity with vegetation heterogeneity only slightly reduced the fit of the model.

For both all (Fig. 2a) and regular (Fig. 2b) users, marsh proximity, water cover, and vegetation heterogeneity produced the best fitting regression model, although replacing vegetation with habitat heterogeneity did not greatly affect results. All independent variables were positively related to species richness (all users $r^2 = 0.87$; marsh proximity $t = 3.79$, $P < 0.007$; water cover $t = 2.97$, $P < 0.02$; vegetation heterogeneity $t = 2.57$, $P < 0.04$; 7 df; regular users $r^2 = 0.85$; marsh proximity $t = 3.73$, $P < 0.007$; water cover $t = 2.45$, $P < 0.04$; vegetation heterogeneity $t = 2.16$, $P < 0.07$; 7 df).

Analysis of changes in vegetative cover at six sites between 1968 and 1981 indicated that most marsh types had stable vegetation patterns. Black Hall River, Great Island, Lord's Cove, and Cromwell Meadows underwent little vegetational change. Wethersfield Meadows showed a small increase in cattail cover, but the extent of high and low salt marsh dropped at Upper Island. Expansion and contraction of vegetation zones in Long Island Sound tidal marshes has been related to long term lunar cycles (Civco et al. 1986). The only consequence of this habitat shift detected during the study period was that populations of Seaside and Sharp-tailed sparrows were reduced, although not eliminated, at transitional marshes (Craig 1990).

Pairwise marsh comparisons.—All three procedures used in cluster analysis on pairwise comparative data (Tables 3, 4) yielded similar groupings

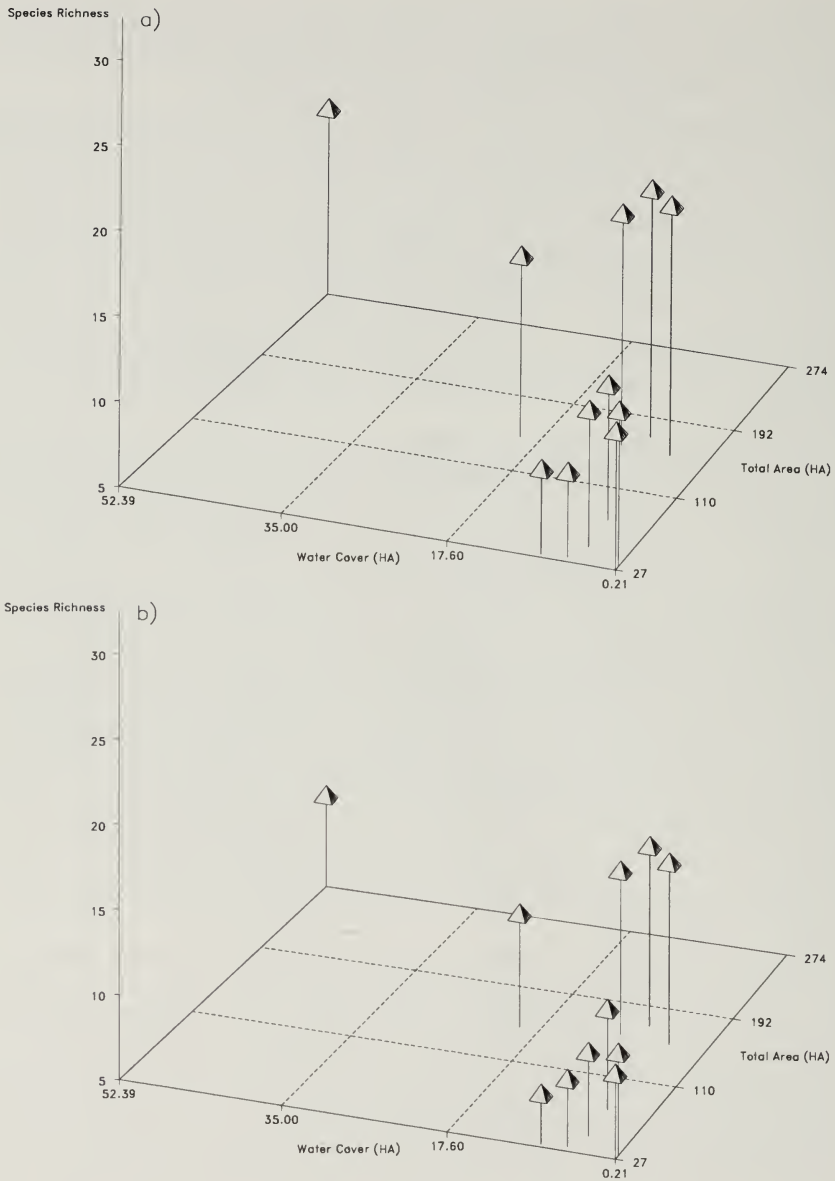

FIG. 1. The relationship between breeder richness, total area, and water cover for (a) all breeders, and (b) regular breeders.

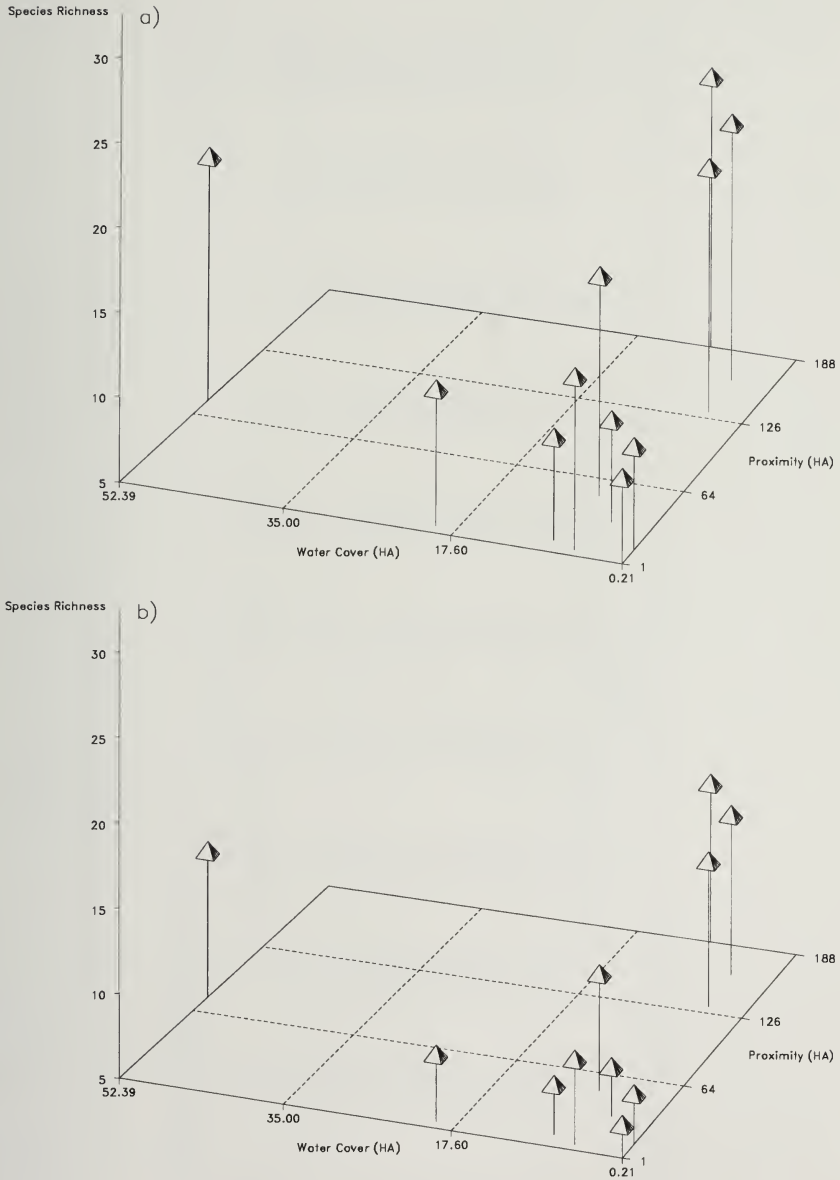

FIG. 2. The relationship between user richness, marsh proximity, and water cover for (a) all users, and (b) regular users.

TABLE 3

PERCENT SIMILARITY IN BREEDER SPECIES COMPOSITION

Site	GI	BH	UI	RR	AP	LC	WC	PM	CM	DM	WE
GI	—	54.5[a]	56.4	78.3	54.5	69.6	39.1	43.5	52.0	44.0	52.2
BH	68.8	—	63.2	63.2	41.2	38.1	37.5	35.3	33.3	30.0	31.6
UI	88.2	68.8	—	90.0	63.2	71.4	45.0	42.9	52.2	37.5	45.5
RR	77.8	58.8	88.2	—	63.2	63.6	45.0	42.9	59.1	43.5	45.5
AP	47.1	42.9	47.1	56.3	—	70.6	69.2	64.3	64.7	52.9	66.7
LC	55.6	43.8	55.6	64.7	75.0	—	50.0	55.6	65.0	47.6	57.9
WC	47.1	42.9	47.1	47.1	50.0	61.5	—	61.5	52.9	50.0	64.3
PM	47.1	33.3	47.1	47.1	63.6	50.0	63.6	—	68.8	66.7	84.6
CM	52.9	40.0	52.9	52.9	72.7	57.1	58.3	90.0	—	66.7	70.6
DM	47.4	35.3	47.4	47.4	61.5	60.0	61.5	61.5	69.2	—	80.0
WE	44.4	23.5	44.4	44.4	46.2	46.7	58.3	72.7	66.7	69.2	—

[a] Above diagonal = all breeders, below diagonal = regular breeders.

TABLE 4

PERCENT SIMILARITY IN USER SPECIES COMPOSITION

Site	GI	BH	UI	RR	AP	LC	WC	PM	CM	DM	WE
GI	—	86.4[a]	86.4	90.5	65.0	85.7	57.1	65.0	70.0	40.0	40.0
BH	76.5	—	82.6	95.2	61.9	81.8	47.8	54.5	59.1	38.1	31.8
UI	70.6	61.1	—	86.4	61.9	81.8	61.9	61.9	59.1	38.1	38.1
RR	75.0	75.0	80.0	—	65.0	77.3	50.0	57.1	61.9	40.0	33.3
AP	41.2	60.0	53.3	57.1	—	68.4	73.3	73.3	68.8	61.5	50.0
LC	55.6	64.7	80.0	73.3	69.2	—	60.0	68.4	65.0	42.1	42.1
WC	33.3	41.2	43.8	37.5	63.6	46.7	—	73.3	68.8	61.5	61.5
PM	38.9	47.1	60.0	53.3	72.7	76.9	58.3	—	92.9	61.5	61.5
CM	38.9	47.1	60.0	53.3	72.7	76.9	58.3	100	—	57.1	57.1
DM	31.3	31.3	33.3	35.7	50.0	46.2	50.0	60.0	60.0	—	77.8
WE	23.5	40.0	33.3	35.7	66.7	46.2	66.7	60.0	60.0	71.4	—

[a] Above diagonal = all users, below diagonal = regular users.

TABLE 5
CLUSTERS OF PAIRWISE COMPARISONS BETWEEN MARSHES

Site	GI	BH	UI	RR	AP	LC	WC	PM	CM	DM	WE
GI	—	3[a]	4	4	1	2	1	1	1	1	1
BH		—	4	4	1	1	1	1	1	1	1
UI			—	3	3	3	1	1	1	1	1
RR				—	3	4	1	1	1	1	1
AP					—	5	2	2	2	1	2
LC						—	1	2	2	1	1
WC							—	3	3	2	2
PM								—	6	2	2
CM									—	2	2
DM										—	3

[a] Numbers refer to membership in clusters 1–6.

of marshes. Results of average linkage cluster analysis are summarized here. For six clusters (Table 5), the largest cluster (27 members) was principally composed of pairwise comparisons between strongly saline, highly tidal influenced (salt, transitional) marshes and freshwater, low tidal influenced marshes. To a lesser extent, saline and brackish cattail marshes were compared. Differences between saline and freshwater marshes principally resulted from the disappearance of certain waterfowl, Clapper (*Rallus longirostris*) and King rails (*R. elegans*), Willets (*Catoptrophorus semipalmatus*), Ospreys, terns, Fish Crows (*Corvus ossifragus*), Seaside and Sharp-tailed sparrows, and several species of waders at freshwater marshes. American Bitterns (*Botaurus lentiginosus*), Soras (*Porzana carolina*), and Wood Ducks, which predominated at freshwater marshes, also contributed to the difference.

Cluster 2 (13 members) consisted primarily of marsh pairs with low salinity and low mudflat areas. Such areas have few waders, gulls, and terns. Cluster 3 (8 members) was predominantly comparisons of sites with similar vegetation and water cover. Cluster 4 (6 members) compared salt vs transitional marshes, and clusters 5 and 6 (1 member each) compared small vs large marshes.

Refuge design.—The number of combined species at the four small freshwater marshes, Whalebone Creek, Pecausett Meadows, Dead Man's Swamp and Wethersfield Meadows, was the same as at the large Cromwell Meadows for all breeders (16) and surpassed Cromwell Meadows for regular breeders (14 vs 10). The four marshes had more species of both all (15 vs 14) and regular (12 vs 10) users than did Cromwell Meadows. Only two breeders occurred no more than occasionally at the small marsh-

es, but six occasional breeders were at Cromwell Meadows. Small marshes had three species of occasional users, whereas Cromwell Meadows had four.

The sole breeders present only at Cromwell Meadows were the Canada Goose (*Branta canadensis*) and Blue-winged (*Anas discors*) and Green-winged teal (*A. crecca*), all occasional breeders there. However, Craig (1990) found Blue-winged Teal summering at the relatively small (25 ha) South Windsor Meadows, a Connecticut River marsh outside the principal study area. Of those breeders present only at small freshwater marshes, the Mute Swan (*Cygnus olor*) was observed only at Whalebone Creek, and the Pied-billed Grebe (*Podilymbus podiceps*) occurred once at Dead Man's Swamp. Among users, only the Glossy Ibis (*Plegadis falcinellus*) occurred solely at Cromwell Meadows, a single occurrence. Users limited to small marshes were the Osprey and Purple Martin (*Progne subis*) which were solely at Whalebone Creek.

DISCUSSION

The principal importance of area in predicting breeder species richness was consistent with findings from other studies of habitat islands (Howe 1984, Brown and Dinsmore 1986). Habitats, which can be more diverse in larger tracts, are thought to be responsible in part for the positive relationship (Rafe et al. 1985). However, in this study the effects of area were separated from those of habitat heterogeneity, which proved weakly or negatively related to species richness. Most breeding species used more than one habitat type (Craig 1990), and therefore increased heterogeneity did not translate into greater species number. Hence, area alone seemed an important determinant of breeder richness.

A species-area relationship may exist in part because the probability of migrant colonization is positively related to total area. Craig (1990), for example, reported that Connecticut River species existing at low densities, such as the Black Rail, King Rail, and Willet often inhabited large marshes. In addition, increased total area may be related to improved habitat quality, as can be the case with forest tracts (Blake 1987). Although Craig (1990) found that even wide-ranging species could occur at the smallest sites, several species of waterfowl and the Northern Harrier predominated at large marshes, suggesting that such sites were superior as habitats.

The negative relationship between water cover and breeder richness was largely a consequence of sites with very high water cover, like Lord's Cove and Cromwell Meadows, having fewer bird species than downriver sites with relatively little water cover. The species added at the downriver marshes (e.g., Clapper Rail, Willet, Seaside and Sharp-tailed sparrows)

are not generally associated with extensive open water. Furthermore, the river channel, present near all sites, may have provided sufficient open water for those species requiring it, thereby minimizing the importance of creeks and ponds present within marsh perimeters. Breeders that frequently feed in or at the edge of open water, such as bitterns and waterfowl, were not eliminated even from sites like Dead Man's Swamp, which had almost no open water. Although open water may benefit certain species (Weller and Spatcher 1965), beyond some threshold level apparently surpassed by all sites in this study, additional open water appears to have no value in increasing bird species richness.

Proximity to additional marsh habitat was important to user richness because certain species clustered around the river mouth where marsh proximity also tended to be greatest. More species, especially wide-ranging ones such as waders, gulls, and terns that must track indefensible, ephemeral prey sources (Krebs 1974) were apparently attracted to areas with more extensive foraging habitat. Traveling between sites may be more effective for foraging than remaining at a single site when searching for ephemeral prey, even when a marsh is large (see also Gibbs et al. 1987). The positive relationship between water cover and user richness further showed that, unlike breeders, users were attracted to areas with more open water in the form of marsh creeks and ponds. Such open water areas were prime foraging sites for species such as waders and terns.

The association of vegetation and habitat heterogeneity with user richness showed that unlike for breeders, the mosaic of habitats present was important to users. The value of such a heterogeneous landscape to users is clear: tidal flats and creeks provide foraging sites for the waders, gulls, terns, and swallows that make up most of the user species, whereas the marsh surface is used for resting and feeding.

Separately analyzing data on all and regular species produced similar results. Hence, the longer term view gained by considering all potentially occurring species yielded little additional information about habitat factors influencing species richness. In contrast, separately analyzing data on breeders and users demonstrated that these species groups have divergent principal habitat requirements. Based on partial regression residual plots (Myers 1986), breeder richness was most strongly influenced by total area and water cover, whereas user richness was most closely related to marsh proximity. Moreover, breeders and users responded inversely to the presence of water cover and environmental heterogeneity.

Clustering pairwise comparisons of marshes showed that saline, strongly tidal marshes strongly differed from freshwater, weakly tidal marshes. Similarity for breeders and users was 23–66%, among the lowest similarity figures computed. Such a distinction is expected in light of the physio-

logical (e.g., Poulson 1969) and behavioral (e.g., Jackson 1983, Burger 1985) adaptations that salt marsh species show for high salinity and tidal fluctuations. However, such factors as marsh proximity, mudflat cover, salinity, and tidal patterns are highly correlated, and therefore, species composition is likely a consequence of the entire suite of differences which distinguish saline and freshwater marshes. The secondary clusters of marsh pairs based on vegetation, water cover, and area suggest that these factors had an influence on species composition as well. Hence, marshes of the same size with similar habitat conditions should attract similar species of birds.

Refuge design.—Even though we demonstrated a species-area relationship for marsh breeders, our findings for the five freshwater marshes are inconsistent with Cole's (1981) theoretical prediction that systems inhabited by good colonizers (i.e., migrants) should have more species on a large habitat island than on several small ones. Combined, the small marshes had a number of breeder and user species equivalent to or greater than that of the large marsh even though each was relatively isolated. Furthermore, they had more regular breeders and users than Cromwell Meadows, which had more occasionally occurring species.

The presence of more occasionally occurring species at Cromwell Meadows may be understood in light of the species-area relationship uncovered for this system. Improved probability of migrant colonization and better habitat quality at large marshes may make species occurring at low densities more likely to colonize them. At least eight of the ten species that occurred occasionally at Cromwell Meadows, and all three of the species unique to this marsh, occurred infrequently in freshwater parts of the river (Craig 1990).

In conclusion, series of small marshes, within the range of sizes considered and within the context of present regional population levels, appeared effective in preserving the species richness of the Connecticut River system. However, they appeared to be less effective than larger marshes in supporting species that exist at low densities. Whether these small marshes can continue to sustain adequate populations to ensure species persistence in the absence of large marshes is as yet unknown.

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AUTUMN OWL MIGRATION AT CAPE MAY POINT, NEW JERSEY

KATHARINE DUFFY[1] AND PAUL KERLINGER[1,2]

ABSTRACT.—During autumn migration 1980–1988, 1042 owls of seven species were captured and banded at Cape May Point, New Jersey. Northern Saw-whet Owls (*Aegolius acadicus*) accounted for 61% of owls banded and Long-eared Owls (*Asio otus*) and Barn Owls (*Tyto alba*) together accounted for another 37%. The migration of barn owls commences in the last days of September, with 90% of captures occurring before 9 November. The seasonal migration of Saw-whet and Long-eared owls is nearly identical, with 90% of captures of these species occurring by 18 and 21 November, respectively. Substantial numbers of the birds migrating through Cape May were adults (after hatch year): 32.5% of Saw-whet, 19.5% of Barn, and 26.1% of Long-eared owls. Adult Saw-whet and Long-eared owls migrated slightly later in the autumn than immatures, whereas adult barn-owls migrated slightly earlier than immatures. Overlap in seasonal timing between age classes was great. More owls were captured during the four hours before sunrise than in the evening, reflecting low altitude flight of migrants seeking hunting or roosting sites after a night's migration. The large number of owls captured in this study demonstrates that the Cape May peninsula is part of a major migratory pathway and is an important stopover area for these animals. *Received 21 June 1991, accepted 5 Nov. 1991.*

Cape May Point, New Jersey, has long been recognized as an important aggregation site for migrating birds, especially raptors during autumn (Stone 1937, Dunne and Sutton 1986). The migration of owls, however, was overlooked until recently (Clark 1972, Duffy 1985). This paper summarizes the results of a banding study of migrating owls at Cape May Point between 1980 and 1988, with specific attention given to species composition, seasonal timing of migration by species, age, and sex classes, and the diel timing of capture of each species.

STUDY AREA AND METHODS

Owls were captured with mist nets and banded at six sites near the end of the Cape May peninsula in New Jersey (38°56′N, 74°58′W; Fig. 1). From 1980 to 1988, banding efforts were initiated each year between 28 September and 10 October (median date = 1 October) and ended between 22 November and 5 December (median date = 26 November). The average number of nights on which nets were used during the nine-year study was 43.7. Use of each of the sites, as well as capture effort (number of nets and net-h) varied from year to year as a result of varying water level, succession of habitats, changes in land ownership, and presence of mammalian predators. The sites are as follows: Site 1.—A "pocket" of brackish marsh (about 1.2 ha) surrounded by upland forest and wetter marsh. The site was dominated by *Spartina patens, Juncus* sp., and *Distichlis* sp. Site 2.—A "pocket" of brackish

[1] Cape May Bird Observatory/New Jersey Audubon Society, P.O. Box 3, 707 East Lake Drive, Cape May Point, New Jersey 08212.
[2] Author to whom reprint requests should be addressed.

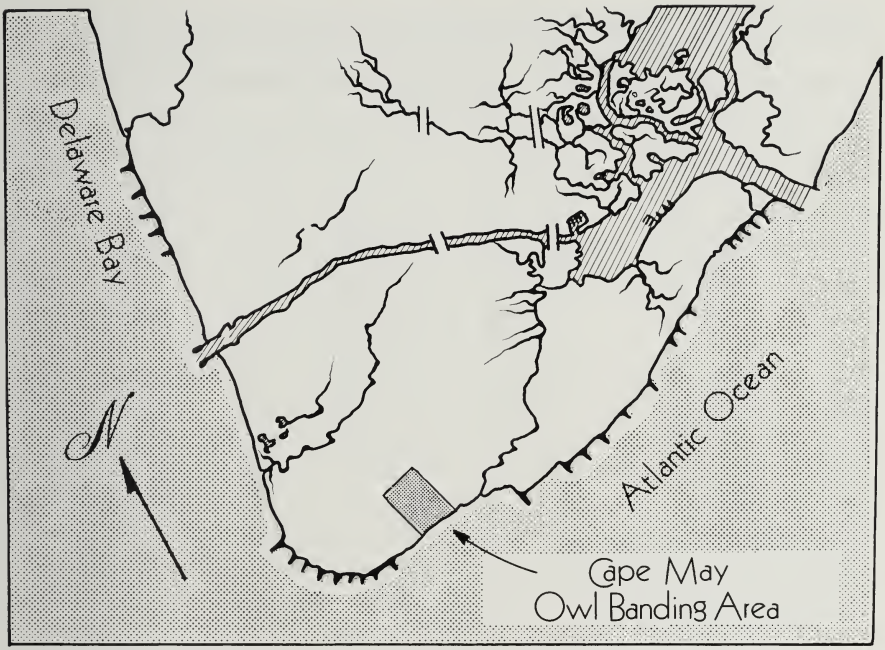


FIG. 1. Map of Cape May Point, New Jersey showing banding area.

marsh bounded on one side by a larger marsh and on the other by upland forest. The size of this "pocket" and vegetation was about the same as Site 1. This site and Site 1 were not used during 1988 when 0.5 m of water was present. Between 1980 and 1988 the size of these "pockets" was reduced by more than 50% as a result of the incursion of *Phragmites communis*. Site 3.—A cultivated field planted with a grassy winter cover crop—surrounded by dry forest. Nets were placed along the west edge of the field approximately 2–3 m from the forest edge. Site. 4.—Red cedar (*Juniperus virginiana*) grove (ca 6 ha) with a partially open canopy—adjacent to wet meadow and a dry forest. Nets and verbails were first used in this field in 1984. Site 5.—Wet and dry meadow with some *Iva*—adjacent to dry forest and ocean dune system. This site was first used in 1984. Site. 6.—Hay field between *Phragmites* marsh and wet forest. This site was used in autumn 1988 when Sites 1 and 2 were flooded. Ten nets were placed along the edge of the field within 2–4 m of upland forest or along the edge of a *Phragmites* marsh.

Between 23 and 52 mist nets were used to capture owls each night (Table 1). The number of net-h each year ranged from 9767 to 26,173. Mist nets were 12 m long and 2.5 m high, usually with 61 mm mesh. Five to ten of the nets used each fall had 121 mm mesh that is more effective for capturing larger owls. A maximum of 12–25 verbail traps were used in a given year. These were placed in grassy areas where owls might hunt from perches. Nets and traps were opened at sunset, closed about 1 h before sunrise, and checked at intervals of 1–2 h. Net checks were more frequent on nights when many owls were captured and when temperatures dropped to <5°C. Nets and traps were not operated on nights when winds were >30 km-h^{-1} or during precipitation or fog. Owls were banded with U.S. Fish and Wildlife Service aluminum tarsal bands, aged, measured (wing chord and mass), and

TABLE 1

SUMMARY OF OWLS BANDED AND NETTING EFFORT AT CAPE MAY POINT, NEW JERSEY, 1980–1988

Year	Saw-whet Owls[a]	Common Barn-Owls[a]	Long-eared Owls[a]	Yearly total[b]	Net-h	Number nights
1980	115 (18.3%)[c]	50 (18.0%)	48 (8.3%)	214	11,375	46
1981	109 (33.0%)	44 (20.5%)	24 (33.3%)	179	15,552	47
1982	53 (58.5%)	20 (25.0%)	14 (14.3%)	89	9767	36
1983	79 (34.2%)	26 (7.7%)	19 (47.4%)	127	12,765	44
1984	8 (87.5%)	1 (0.0%)	14 (64.3%)	29	26,173	49
1985	30 (13.3%)	4 (0.0%)	8 (25.0%)	49	23,870	40
1986	78 (23.1%)	15 (13.3%)	5 (20.0%)	104	17,329	49
1987	72 (43.1%)	7 (28.6%)	16 (62.5%)	96	17,119	44
1988	87 (34.5%)	13 (38.5%)	55 (14.5%)	155	12,413	38
Totals	631 (32.5%)	180 (19.5%)	203 (32.2%)	1042[b]	146,363	393
Mean	70.1	20	22.6	115.8	16,263	43.7
SD	34.9	17.2	17.4	56.3	5287	4.4

[a] Percentage of adult (AHY) birds captured.
[b] Totals include one Short-eared Owl (*Asio flammeus*), 19 Eastern Screech-Owls (*Otus asio*), seven Great Horned Owls (*Bubo virginianus*), and one Barred Owl (*Strix varia*).
[c] Percentages are in parentheses.

released. Owls were aged as adults (AHY = after hatch year) by the presence of more than one generation of flight feathers or as immatures (HY = hatch year) by the presence of only one generation of flight feathers. Other techniques for determining age were from Anonymous (1980).

RESULTS

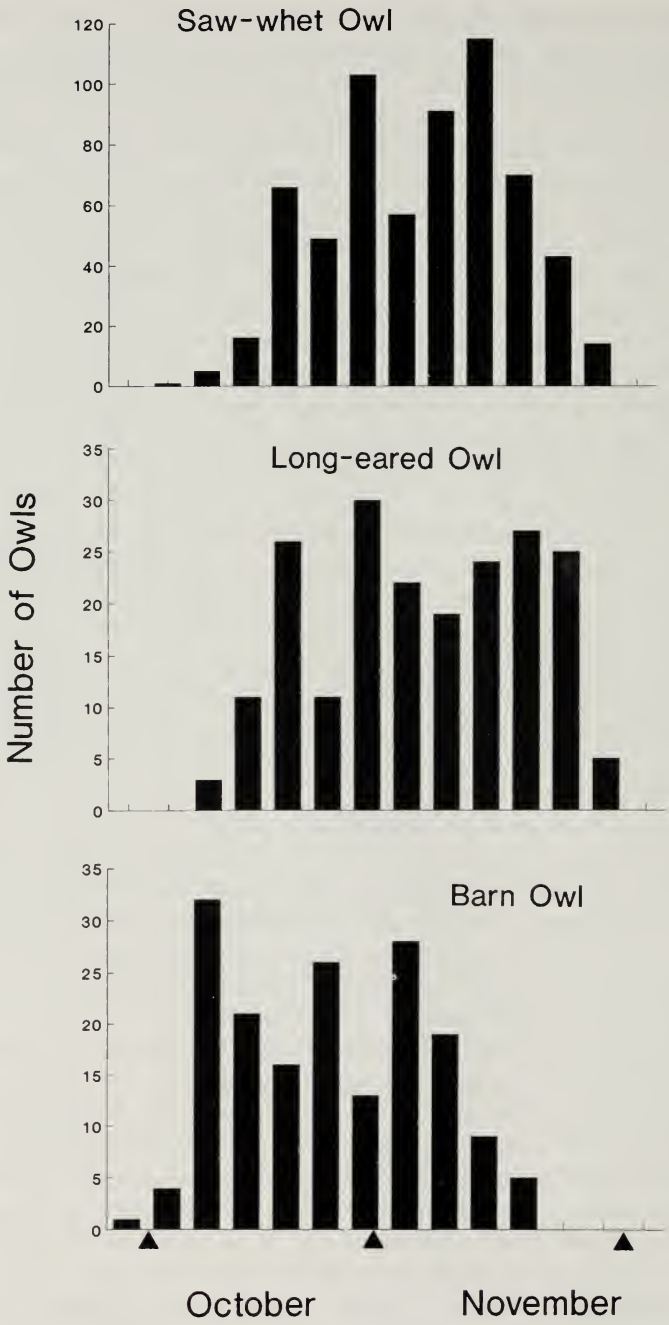
Species composition.—In the nine years of owl banding reported here, 1042 individuals of seven species were captured (Table 1), an average of 116 owls per year. The numbers of owls captured varied among years with only 29 being captured in 1984 and 214 captured in 1980. Three species accounted for more than 97% of all owls captured. Northern Saw-whet Owls (*Aegolius acadicus*) were most numerous (60.6%), followed by Long-eared Owls (*Asio otus*—19.5%) and Barn Owls (*Tyto alba*—17.3%). The remaining 28 owls (Table 1) were from four species. The proportion of adult (AHY) birds captured varied among species. These percentages include a small number of birds (6 Long-eared Owls, 12 Saw-whet Owls, and 3 barn owls) for which age determination was not made or was equivocal. A slightly greater percentage of Long-eared (26.1%) and Saw-whet owls (32.5%) were adults than were barn owls (19.5%). In 1984, when owl captures numbered about one-quarter the mean capture rate for the nine-year study, adults accounted for 87.5% of Saw-whet Owls and 64.5% of Long-eared Owls. These percentages are higher than for any

other year of the study, although there appears to be no relation between the numbers of owls banded and the percentage of adult birds.

Seasonal timing of migration.—Owl migration through Cape May commences in September and continues into December (records of Cape May Bird Observatory). Prior to October and after November, however, the number of migrants is small in comparison with the numbers captured during our study. An exploratory study before 1980 demonstrated the futility of attempting to capture owls during September and December. Large numbers of owls do not begin to migrate through Cape May until the second week in October. Capture rates before the second week of October are so low as to discourage banding efforts (Fig. 2). A few barn-owls migrate before the initiation of autumn banding activities (records of Cape May Bird Observatory). In general, barn-owls migrate earlier than Saw-whet and Long-eared owls by about two weeks (Fig. 2). Nearly 90 (89.1%) percent of barn-owl captures occurred between 6 October and 9 November (Fig. 2), with 50% of the flight passing by 23 October. By 9 November, about 90% of barn owls had passed. The migration of Saw-whet and Long-eared owls commenced in mid-October. Approximately ninety percent of Saw-whet Owls passed between 16 October and 19 November, whereas 90% of Long-eared Owls passed between 16 October and 24 November (Fig. 2). The mid-migration (50% of captures) dates for Saw-whet Owls was 7 November, with 90% passing by 18 November. For Long-eared Owls mid-migration occurred on 4 November, and 90% had passed by 21 November. Thus, the migration period for these species in Cape May is virtually identical.

Adult barn-owls seem to migrate, on average, a few days earlier than immatures (Fig. 2). By the end of October, 85.3% (29 of 34) of the adult barn-owls observed had been captured, but only 60.6% (83 of 137) of the immatures had been captured. No adults were noted after 9 November, whereas 14 (10.2%) immatures were noted after this date. The difference in frequencies of adult and immatures between October and November, though small, was significant ($\chi^2 = 7.26$, df = 1, $P < 0.01$).

For both Saw-whet and Long-eared owls, adults migrated slightly later in autumn (Fig. 2). A slight, but significant difference was noted among the frequencies of adult and immature Saw-whet Owls captured during October and November ($\chi^2 = 7.46$, df = 1, $P < 0.01$). Slightly more than thirty percent (30.7%) of all adult Saw-whet Owls were captured in October as opposed to 42.1% of immatures. After 10 November the percentages changed to 43.4% of all adults and 35.1% immatures. A more obvious difference was noted among Long-eared Owls in which only 9.4% of adults (5 of 53) migrated in October compared with 52.1% of immatures (75 of 144). Two-thirds of all adults of this species migrated after 10 November,


Saw-whet Owl
120
100
80
60
40
20
0
Long-eared Owl
35
30
25
20
15
10
5
0
Number of Owls
Barn Owl
35
30
25
20
15
10
5
0
October
November

whereas only 29.2% (42 of 144) of immatures migrated after this date. When the frequencies of adults in October and November were compared statistically, the differences were significant ($\chi^2 = 29.20$, df = 1, $P < 0.01$). There was far more overlap among the age groups of Saw-whet Owls. Overall, the differences for Long-eared Owls appeared to be more marked than among Saw-whet Owls and barn-owls.

Regression analysis of wing chord on date revealed no trend suggestive of a seasonal difference in migration timing between the sexes. Because females have longer wing chords than males (Snyder and Wiley 1976), we reasoned that if a sexual difference in seasonal timing of migration occurred, it would be revealed by regression analysis. We conducted three regressions for each of the three species; one for after hatch year (AHY), one for hatch year (HY), and one for AHY and HY birds combined. Not one of the nine regressions revealed a hint of any seasonal differences in migration timing between the sexes. Maximum regression coefficients accounted for less than 0.025 (2.5%) of the variance. Sample sizes are slightly smaller than those given for each species in Table 1 because wing chords for several individuals were not measured.

Diel timing of migration.—To determine if there was a statistically significant diel pattern (departure from equiprobability) of capture frequency, nights were divided into three, roughly equal (4 h) periods. Among all three species of the common migrants, more birds were captured in the period just prior to dawn than in either the middle of the night or early in the evening (Fig. 3). The trend is particularly strong for both Long-eared Owls ($\chi^2 = 58.87$, df = 2, $P < 0.01$) and barn owls ($\chi^2 = 63.19$, df = 2, $P < 0.01$) in which 60.3% and 65.7% were captured in the four hours preceding sunrise. The percentages captured during the first and second four-hour periods after sunset were roughly the same for these species. The trend is present but less marked among Saw-whet Owls ($\chi^2 = 14.90$, df = 2, $P < 0.01$) for which only 40.2% of the captures were made in the four hours preceding sunrise.

DISCUSSION

The significance of the Atlantic Coast as a migratory pathway with stopover sites for owls has been overlooked. In his classic work about the ornithological significance of Cape May, Stone (1937) omitted mention of the substantial owl migration, although he did say that the barn owl

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FIG. 2. Seasonal timing of migration patterns for adult (hatched) and immature (solid) Saw-whet Owls, Long-eared Owls, and Barn Owls during autumn migration at Cape May Point, New Jersey. Each bar represents a five-day period.

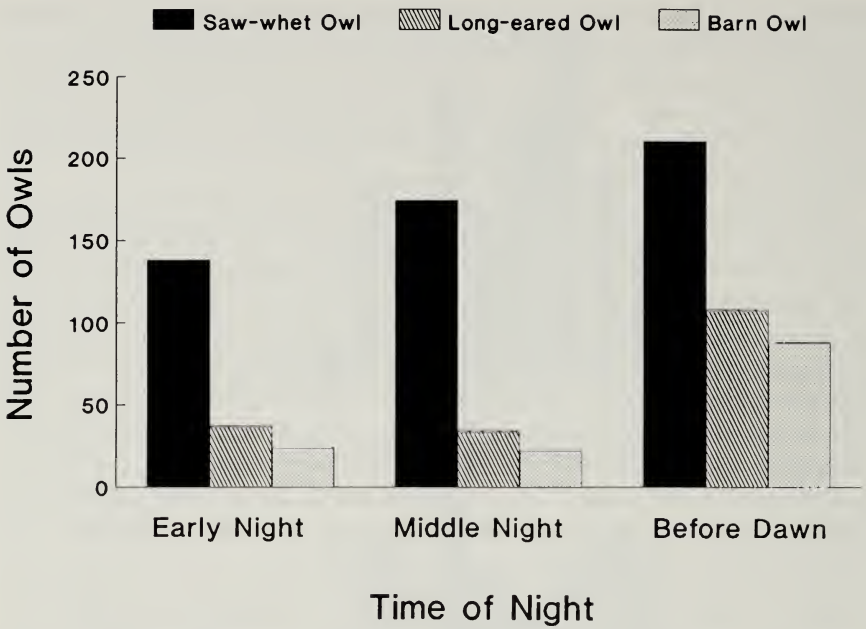

FIG. 3. Diel timing of captures of Saw-whet Owls, Long-eared Owls, and Barn Owls at Cape May Point, New Jersey, 1980–1988. The three periods (early, middle and late) represent roughly equal (about 4 h) portions of the night.

was a "regular autumn transient . . . occurring most frequently during October." Like raptors, songbirds, and many other species of birds, numbers of owls are concentrated near the tip of the Cape May peninsula. Unlike the concentrations of raptors and songbirds at Cape May and along the New Jersey coast, a larger proportion of the owls are adults. The percentage of adults among the raptors and songbirds that migrate through Cape May and along the Atlantic coast rarely exceeds 15% (unpubl. data, Cape May Bird Observatory; Murray 1966). The percentage of adults among the owls banded was between 19.5 and 32.5% for the three most common species. Few migrating owls are banded at more southerly latitudes than our station and at no other location is there known to be a concentration of migrating barn owls. The latter finding was first reported by Duffy (1985), and this report lends credence to her contention that there is a seasonally predictable migration of this species. Most owl banding projects that focus on capturing migrating owls are to the north, most by several hundred kilometers (mostly north of 43°N) at sites such as Whitefish Point, Michigan (Carpenter 1987); Braddock Bay, New York (J. Dodge, pers. comm.); Cedar Grove, Wisconsin (Mueller and Berger 1967); and Long Point, Ontario (Weir et al. 1980).

With respect to diel timing of captures, our data show that owls are more likely to be captured in the four h preceding dawn. This is similar to the findings of Weir et al. (1980) for Saw-whet Owls. Russell et al. (1991) relied on visual observations (aided by an image intensifier) at Cape May Point to document that the largest numbers of migrating owls occur in the first few hours after sunset. It is possible that both observations are correct. Like other nocturnal migrants (Kerlinger and Moore 1989), owls may initiate migration within the first hour following sunset. Because our nets seldom exceeded 2.5 m in height, we suggest that the owls we captured were not actively migrating. Instead these owls had, more than likely, ceased migrating on that night and were either foraging or seeking a roosting site.

From our data we make two tentative conclusions. First, it is possible that barn owl populations are declining. A steady decline of barn owls between 1980 and 1988 was evident. The decline is even greater when data from a casual owl banding study in Cape May in the late 1970s is considered. In the latter study, up to 100 barn owls were banded in one season (W. S. Clark and M. Eloranta, unpubl. data). Because some of the best habitats for banding barn owls have changed so much as to preclude banding, we can only suggest that fewer individuals of this species now migrate through Cape May.

Finally, the differences in seasonal timing of migration between the ages should be considered suggestive. Although the differences in seasonal timing between adults and immatures were significant for all species, the distributions of passage dates overlap almost completely (Fig. 2). Thus, several more years of data are needed to confirm our findings.

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Wilson Bull., 104(2), 1992, pp. 321–326

SHORT COMMUNICATIONS

Food habits of Mexican Spotted Owls in Arizona.—The Spotted Owl (*Strix occidentalis*) is most common in mature and old-growth coniferous forests throughout much of its range (Forsman et al. 1984, Laymon 1988, Ganey and Balda 1989a, Thomas et al. 1990). Proximate factors underlying habitat selection in Spotted Owls are understood poorly. Abundance and availability of food, however, may be a key factor influencing habitat selection in birds in general (Hilden 1965) and in owls in particular (Southern and Lowe 1968). In addition, prey abundance has been implicated as an important influence on reproduction in many owls (e.g., Rusch et al. 1972, Lundberg 1976, Wendland 1984).

In many areas, only two or three species of prey comprise 70–90% of prey biomass in Spotted Owl diets (Thomas et al. 1990:205–215). Understanding the ecology of these key species of prey could contribute greatly to understanding the ecology of the Spotted Owl. Despite this possibility, little is known about the diet of the Mexican subspecies of the Spotted Owl (*S. o. lucida*), which inhabits the southwestern United States and Mexico (Forsman et al. 1984). Previous reports suggest that Mexican Spotted Owls prey heavily on woodrats (*Neotoma* spp.) and also take other small mammals, birds, reptiles, and invertebrates (Ligon 1926, Marshall 1957, Kertell 1977, Wagner et al. 1982, Ganey et al. 1988, Duncan and Sidner 1990). These reports are based on small samples from restricted geographic areas, however, and may not reflect the full range of the diet in the southwest.

Information on food habits of the Mexican Spotted Owl was gathered at locations scattered throughout Arizona from 1984–1990. This is the first broad survey of food habits of Spotted Owls in the Southwest, and could aid in designing future studies on both feeding ecology of Mexican Spotted Owls and the prey populations on which they depend.

Methods.—Pellets and prey remains were collected beneath Spotted Owl roost and nest sites in habitats ranging from mid-elevation (1125 m) rocky canyons to high-elevation (2930 m) mixed-conifer forests. Remains were collected opportunistically whenever they were found. All remains collected during a visit to a site were treated as a single sample because remains of large vertebrates can appear in more than one pellet (Forsman et al. 1984). If some pellets appeared markedly older than others, however, I identified two samples as containing old and recent pellets, respectively (Forsman et al. 1984). Older pellets were dry, dusty, and partially disintegrated.

All prey remains collected were dated and grouped by five geographic regions: the San Francisco Peaks, approximately 3 km north of Flagstaff; Walnut Canyon, approximately 4 km southeast of Flagstaff; Black Mesa, on the Navajo Reservation in northeastern Arizona; the White Mountains of east-central Arizona; and southeastern Arizona (including the Santa Catalina, Santa Rita, Huachuca, and Chiricahua Mountains). Pellets were collected from three to 11 pairs of owls within each geographic area. Lumping of pellets from adjacent pairs may have masked variation in dietary composition among individual pairs (Laymon 1988), but was necessary because pellets collected from areas of overlap between adjacent pairs could not always be unambiguously assigned to a particular pair. Also, sample sizes were too small to characterize the diet adequately for most individual pairs.

Vertebrate prey were identified by comparison with specimens in the Northern Arizona University Museum of Vertebrates (NAUMV), using skeletal remains or feathers. The minimum number of individuals of each species was determined in each sample by counting skulls, right or left rami, or other identifiable skeletal remains (Forsman et al. 1984).

Invertebrates were identified and counted using mandibles, femurs, wings, or fragments of exoskeleton. In samples containing beetle legs, I estimated the minimum number of

individuals by counting all legs and dividing by six. Biomass of each species in the diet was estimated by multiplying the number of individuals by mean wet body mass. Body mass estimates were obtained from the literature (Steenhof 1983, Forsman et al. 1984, Severson and Hayward 1988) or from specimen records (NAUMV). A table of common and scientific names for all prey items, along with estimates of body mass and sources for those estimates, is available from the author.

The opportunistic nature of the sampling limited the types of analyses I could conduct. Because sites were visited with differing frequencies in different years and seasons, unknown biases may exist within the data if there are interactions among region, season, and year. A preliminary log-linear analysis indicated that such interactions were present in the data, suggesting that in further comparisons all but one factor should be held constant.

Collections of ≥100 items per treatment were assumed necessary to characterize the diet for statistical comparisons (after Marti 1988). Sample sizes for most combinations of region, season, and year were inadequate by this criterion. Therefore, I view these data as useful primarily to describe some aspects of the feeding ecology of Spotted Owls, and have largely avoided statistical comparisons.

Results.—Between May 1984 and August 1990, I identified 1434 prey items from pellets or kills of 34 pairs of owls. The diet included at least 19 species of mammals, seven species of birds, two species of reptiles, and an unknown number of insect species. Vertebrates dominated the diet in all five regions, comprising 84–96% of total prey and 99% of prey biomass (Table 1). Mammals accounted for 73–96% of total prey and 91–99% of prey biomass. Owls consumed prey ranging in mass from beetles (Coleoptera) and moths (Lepidoptera) (ca 1 g) to adult cottontail rabbits (*Sylvilagus* spp.; ca 650 g). Mean prey mass ranged from 63–118 g in various regions.

Woodrats, white-footed mice (*Peromyscus* spp.), and voles (*Microtus* spp.) accounted for 61–83% of the total prey and 59–88% of total biomass in various regions (Table 1). Cottontails and pocket gophers (*Thomomys* spp.) accounted for another 3–14% of total prey and 7–36% of total biomass. Birds and reptiles contributed little to prey numbers or biomass except in Southeast Arizona. Insects were relatively common in the diet (3–16% of total prey) but contributed little to prey biomass. Diurnally active mammals such as squirrels and chipmunks (Sciuridae) accounted for <3% of total prey or biomass.

There appeared to be differences in the diet among regions within Arizona (Table 1), but after controlling for season and year, sample sizes were insufficient for statistical comparisons among regions. In general, woodrats and white-footed mice were common in the diet (>10% of total prey) in all regions. Voles were common in three regions, but were uncommon on Black Mesa, and did not appear in the diet in Southeast Arizona. Bats (Chiroptera), birds, and insects were most common in the diet in Southeast Arizona, and reptiles were observed in the diet only in that region.

I was able to compare dietary composition among years in only one region (Walnut Canyon, 1984–1987) and then only after combining prey categories to avoid low expected values. Dietary composition during the breeding season varied significantly among years (Table 2; $\chi^2 = 45.7$, df = 12, $P < 0.001$; N = 4 years and 655 items). The diet also appeared to vary among years on the San Francisco Peaks (Table 2), but sample sizes were too small for meaningful comparisons. Mammals comprised the majority of the diet in all regions in all years.

I could not compare dietary composition among seasons because most data (79%) were collected during the breeding season. In general, fewer bats and insects were taken during the nonbreeding season (1 September–28 February; Ganey and Balda 1989b) than during the breeding season, whereas the most common mammalian taxa were taken in relatively high numbers in both seasons.

TABLE 1

DIETARY COMPOSITION OF MEXICAN SPOTTED OWLS IN FIVE GEOGRAPHIC REGIONS IN ARIZONA, 1984–1990[a]

Prey type[b]	Walnut Canyon		San Francisco Peaks		White Mountains		Black Mesa		Southeast Arizona	
	Prey (711)	Biomass (79,037)	Prey (276)	Biomass (17,455)	Prey (157)	Biomass (12,847)	Prey (89)	Biomass (10,492)	Prey (201)	Biomass (13,055)
Neotoma	33.1	50.0	18.5	49.1	17.8	36.6	57.3	81.7	22.4	57.9
Peromyscus	26.3	5.7	33.0	12.5	20.4	6.0	23.6	4.8	38.8	14.3
Microtus	14.3	4.5	27.2	15.0	37.6	16.1	2.2	0.7	0.0	0.0
Sylvilagus	8.4	29.6	1.1	6.7	5.1	24.3	1.1	3.7	2.0	11.9
Thomomys	6.0	6.1	5.1	9.1	5.7	7.9	3.4	3.2	0.5	0.9
Bats	1.7	0.2	0.0	0.0	0.0	0.0	2.2	0.3	5.5	1.5
Other mammals	3.0	2.3	3.3	4.4	5.7	6.0	5.6	4.1	3.5	4.6
Birds	2.5	1.5	2.9	3.1	3.8	3.1	1.1	0.6	7.5	7.7
Reptiles	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	0.9
Insects	4.6	<0.1	9.1	<0.1	3.8	<0.1	3.4	<0.1	16.4	0.3
Average prey mass (g)	111		63		82		118		65	

[a] All values in columns are percentages and the total number of prey and total biomass (g) in parentheses.
[b] Numbers of pairs represented: Walnut Canyon = 3; San Francisco Peaks = 7; White Mountains = 11; Black Mesa = 3; Southeast Arizona = 10.

TABLE 2

ANNUAL VARIATION IN THE DIET OF SPOTTED OWLS IN TWO REGIONS IN ARIZONA. VALUES REPRESENT % OF TOTAL PREY COLLECTED DURING THE BREEDING SEASON (1 MARCH–31 AUGUST)

Site	Year	N	Prey type				
			Neotoma	Peromyscus	Microtus	Other mammals	Other
Walnut Canyon	1984	116	42.2	25.0	10.3	12.9	9.5
	1985	249	21.7	28.1	20.1	19.3	10.8
	1986	188	41.0	27.1	10.1	19.7	2.1
	1987	102	32.4	24.5	13.7	24.5	4.9
San Francisco Peaks	1986	61	18.0	24.6	16.4	18.0	23.0
	1987	110	10.0	56.4	23.6	6.4	3.6
	1988	79	25.3	10.1	44.3	7.6	12.7

Discussion.—Small mammals dominate the diet of Spotted Owls in Arizona, with a few species comprising the bulk of the diet. This was also generally true in other areas where food habits of Spotted Owls were studied (e.g., Barrows 1980, Wagner et al. 1982, Forsman et al. 1984, Laymon 1988). In Arizona, the most common prey groups (woodrats, white-footed mice, and voles) were common in the diet in most regions, both seasons, and all years.

The range of average prey masses in Arizona (63–118 g; Table 1) fell within the range reported by Forsman et al. (1984) for Spotted Owls in different regions in Oregon (54–150 g). Barrows (1980) reported an average prey mass of >100 g for Spotted Owls in California.

Spotted Owls prey heavily on woodrats in many areas (e.g., Barrows 1980, Wagner et al. 1982, Forsman et al. 1984). The relative abundance of woodrats in the diet appears to vary as a function of habitat, however. For example, Spotted Owls in Oregon preyed heavily on woodrats in xeric forests. In more mesic forests, where woodrats were uncommon, northern flying squirrels (*Glaucomys sabrinus*) comprised the bulk of the diet (Forsman et al. 1984, Thomas et al. 1990). Similar patterns occurred in Arizona. In northern Arizona, Spotted Owls ate fewer woodrats and more voles in mesic high elevation forest areas (San Francisco Peaks and White Mountains) than in more xeric areas dominated by rocky canyons (Walnut Canyon and Black Mesa). Most woodrats taken were probably either Mexican (*N. mexicana*) or white-throated (*N. albigula*) woodrats, based on distribution and habitat use of these species. These species are most abundant around rock outcrops and cliffs (Goodwin and Hungerford 1979, Hoffmeister 1986), habitats far more common in the Walnut Canyon and Black Mesa regions than in the San Francisco Peaks and White Mountains regions. In contrast, most voles taken were probably Mexican (*M. mexicanus*) or long-tailed (*M. longicaudus*) voles, species that are more abundant in the grassy understories of forests in the latter regions (Hoffmeister 1986). The importance of habitat as a factor contributing to variation in dietary composition was also suggested by the differences in the diets of owls in Walnut Canyon and on the San Francisco Peaks, two regions that were close geographically but very different in habitat composition.

The annual variation in the diet may indicate that Spotted Owls respond to changes in prey availability among years. Forsman et al. (1984) also noted annual variation in the diet in Oregon. In that study, as in Arizona, the major prey taxa were generally well represented

in all years, although relative rankings changed somewhat. Neither study was based on systematic sampling, however, and sampling bias may have contributed to the apparent annual variation (Forsman et al. 1984).

Analyses of food habits based on pellet analysis may be subject to bias. I probably underestimated the number of insects in the diet, because remains of such animals are less likely to be found in pellets than vertebrate remains. The proportion of insects in the diet would have to increase greatly in order for insects to contribute much to prey biomass, however.

Future studies of food habits of Spotted Owls should attempt to gather larger samples from individual pairs to examine variation among pairs. Systematic sampling of particular pairs across seasons and years could provide useful information on the extent of temporal variation in dietary composition. Studies that quantified abundance of small mammals would be particularly useful, as they would allow comparisons of use and availability of various taxa. Future studies should also examine habitat relationships of selected small mammals to provide insight into habitat features important to population levels of prey species. In Arizona, particular attention should be paid to factors influencing the distribution and abundance of woodrats, white-footed mice, and voles because of their abundance in the diet.

Because small mammals dominate the diet of Spotted Owls in Arizona, management activities that reduce small mammal populations in areas inhabited by Spotted Owls should be avoided. In most cases, this probably means that adequate amounts and types of downed wood should be maintained for hiding cover (Goodwin and Hungerford 1979). The effects of livestock grazing on herbaceous vegetation and vole abundance should also be evaluated where Spotted Owls occur.

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JOSEPH L. GANEY, *Dept. of Biological Sciences, Northern Arizona Univ., Flagstaff, Arizona 86001.* (Present address: *Rocky Mountain Forest and Range Experiment Station, 700 S. Knoles Drive, Flagstaff, Arizona 86001.*) *Received 26 Aug. 1991, accepted 18 Nov. 1991.*

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Nestling growth rates of Short-eared Owls.—The Short-eared Owl (*Asio flammeus*) is a widely distributed ground-nesting species (Burton 1973). Nests are difficult to locate, and consequently few data are available concerning the owl's breeding biology (Clark 1975, Cramp 1985). Clark (1975) reported nestling growth for three captive Short-eared Owls from Manitoba, Canada. Hagen (1952) provided growth data for two nestling Short-eared Owls from Norway. Wijnandts (1984) reported growth models for Hagen's data and perhaps from some unpublished data. Unfortunately, it is unclear if the unpublished data were for masses or some other category; the numbers were not stated. Here we describe growth rates of wild nestling Short-eared Owls. To our knowledge, this is the first report of such data for North America.

Study area.—Nantucket Island is located approximately 32 km south of Cape Cod, Massachusetts. The island (130 km^2) consists of moraines and out-wash plains from Pleistocene glaciation (Woodsworth and Wigglesworth 1934), and is unique in its composition of maritime heaths and "moorlands" (Tiffney and Eveleigh 1985). There are no native mammalian predators, but feral and domestic dogs and cats do occur.

Methods.—Nine nests were located during April and May 1985. We located nests by searching the grassland area where male Short-eared Owl courtship flights took place. We weighed nestlings at four nests every other morning until they dispersed from their nests, using 100-, 300-, and 500-g capacity Pesola scales with increments of 1.0, 2.0, and 5.0 g, respectively. Short-eared Owl eggs hatch asynchronously, and nestlings vary in age and size. We did not mark nestlings because they were distinctive until just prior to leaving their nests. Nestlings were banded when approximately 10-days-old with United States Fish and Wildlife Service aluminum bands. By the third week of May, all eggs had hatched. Nests were not visited during inclement weather.

Ricklefs (1983) stated that, in describing bird growth, the most straightforward approach is to fit the growth data to models with a few interpretable parameters. He further stated that growth among organisms can be compared intraspecifically and interspecifically, with each species having characteristic growth patterns. To describe Short-eared Owl growth, we used a logistic growth model for each nestling. Comparisons of growth rates between nests were made using these selected models. We did not assume that owl nestlings grew at the same rate; therefore, data were not pooled from individual nests.

Preliminary model fitting of various forms of the Richards' (1959) curve was used to choose the logistic model. The Richards' equation (Richards 1959) is $W(t) = [A^{m-1} + Be^{-kt}]^{1/(1-m)}$ where W is weight, t is time, 1/A is the asymptotic value of W, m is a shape parameter, B is a parameter related to the time of origin, and k is a constant proportional to overall growth rate. The logistic model is obtained by setting m = 2, (i.e., $W(t) = 1/(A + Be^{-kt})$. After the logistic form of the Richards model was determined to be sufficient, we used it for all data.

Parameter estimates were computed using the linearization method (Draper and Smith 1981). Model fit was assessed by plotting residuals against time (in days) and by inspecting the plots for evidence of bias (systematic over-or-under prediction) and non-constant variance.

The model which minimized the median absolute deviation of all weights about the fitted regression equation was chosen as a representative growth model for a given nest. Since the sample median minimizes the sample sum of the absolute deviations, we refer to this representative model as the median model. We did not feel enough data were collected to estimate asymptotic weights.

Results.—We used data from 18 nestlings from four nests (total of 110 weighings). Parametric estimates for all nestlings were similar among all nests except Cisco Beach, which only incorporated data from two nestlings (Table 1).

None of the models suffered from a notable degree of bias. The magnitude of all residuals tended to increase with time for all models. This evidence of non-constant variance does not detract from use of these models as descriptors of observed growth. This analysis has shown consistency among growth curves from three of four nests (Fig. 1). The remaining model from the Cisco Beach nest may be in error since hatching was estimated rather than observed.

For each of the median models, we estimated absolute body mass increments over four five-day-periods. These increments were chosen because they approximated nestling growth curves. Body mass increments were similar among all nests except Cisco Beach. The mean predicted body mass at hatching for nests 1, 3, and 4 was 14.7 g. These values were similar

TABLE 1

LOGISTIC GROWTH MODEL PARAMETER ESTIMATES FOR NESTLINGS AT FOUR NESTS

Nestlings	Weighings	Parameter A[a]	Parameter B[b]	Parameter K[c]	Mean absolute deviation
Miacomet nest					
1	7	0.00304	0.0709	0.293	20.48
2	6	0.00351	0.0820	0.314	19.26
3	7	0.00433	0.1000	0.361	30.70
4*	8	0.00308	0.0913	0.307	16.20
5	8	0.00503	0.0899	0.387	45.31
6	7	0.00456	0.0907	0.309	48.81
Cisco Beach nest					
1*	7	0.00205	0.0429	0.187	24.95
2	8	0.00246	0.0735	0.263	27.14
Ram Pasture nest					
1	6	0.00380	0.0828	0.354	14.63
2*	5	0.00308	0.0828	0.304	12.81
3	4	0.00392	0.0799	0.375	19.52
Golf course nest					
1	6	0.00313	0.0771	0.325	44.38
2	5	0.00338	0.0771	0.323	45.78
3	5	0.00304	0.0680	0.316	48.82
4	4	0.00350	0.0749	0.337	43.93
5*	6	0.00320	0.0949	0.330	40.80
6	5	0.00329	0.1179	0.323	50.86
7	6	0.00594	0.0473	0.302	130.36

[a] Asymptotic value of weight (1/A).
[b] Parameter related to time of origin.
[c] K is a constant proportional to overall growth rate.
* Median growth model for each nest.

to the actual mean hatching body mass data (16.0 g, N = 8). There were no hatching data from nest number 2 and the value (26.6 g), estimated from the model represents day two (26.6 g), which is actually the predicted body mass for day two. According to the models, nestling Short-eared Owls gained an average of 8 g of body mass per day for the first five days of life, 19 g per day during the next five days, 21 g per day during the next five days, and 12 g per day during the last five days for which we have data (Table 2, Fig. 2). The Cisco Beach nest growth rates differed from the other nests. The predicted body mass gain for the Cisco Beach nest was less than for other nests for days 6–10 and more for days 16–20. It is interesting that the two nestlings from Cisco Beach nest grew faster in the fourth period (days 16–20) than nestlings from the other three nests (Table 2). We wonder if the small brood size, hatching date error or "compensatory growth" (I. L. Brisbin, pers. comm.) influenced these results.

Nestlings number 2 and 7 from Golf Course nest showed a decrease in body mass. This may be explained by: (1) the female owl's disappearing from the nest during the nestlings'

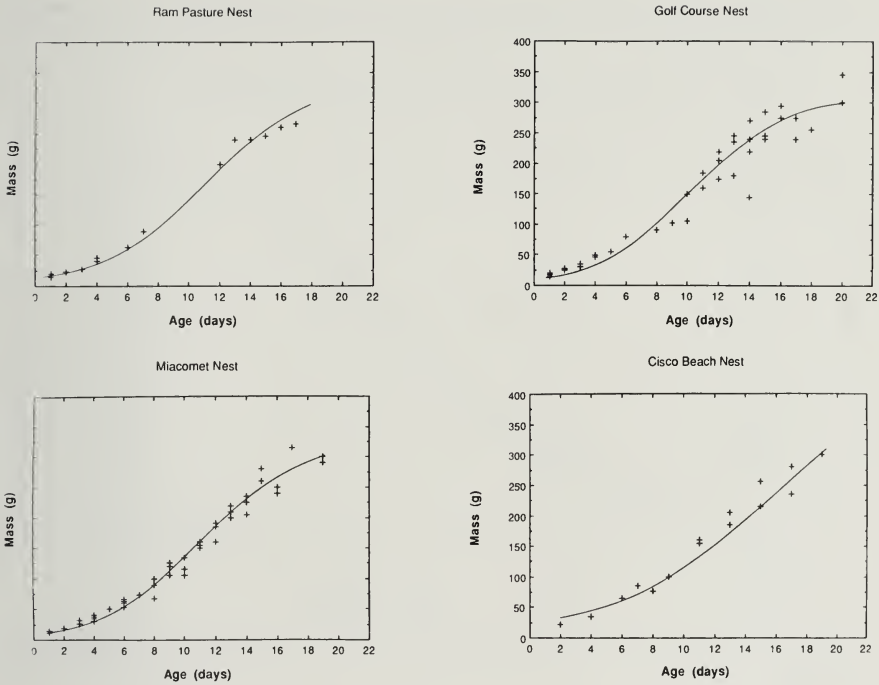

FIG. 1. Median growth models for all nests.

second week of growth. This may have put additional pressure on the male to provision food for seven nestlings; (2) we made errors in data recording; (3) other unknown factors.

Nestling growth was most rapid during periods 6–10 and 11–15. Nestlings gained almost twice the body mass during period 6–10 and almost three times the body mass during period 11–15, when compared with period 1–5 (Fig. 2). During the fourth period, body mass gains slowed as the owls gained an average of 12 g per day. Sexes of the nestlings could not be determined, so differential growth by sex is not reported.

In this study, flightless nestlings dispersed form their nests when approximately 16 days old ($\bar{x}$ = 15.7, SD = 1.11, range 14–17, N = 18). These pre-fledging dispersers moved up to 55 m from their nests for approximately a two-week period prior to their first flights. Pre-fledge dispersal coincided with growth period 11–15, at which time the owls gained most of their nestling body mass. The owls fledged when approximately 30 days old, although reluctant to fly initially. They also may have been influenced to fly by our activities.

Discussion.—Nice (1962) classified owls as semi-altricial. Short-eared Owls live in open habitats and nest on the ground. The nestlings are nidicolous. These habitats are characterized by food resources and climatic conditions which may have much annual variation (Cody 1985). Reasons for pre-fledging dispersal strategies in the Short-eared Owl have not been discussed in the literature. We believe that selective pressure favors rapid growth and development in nestling Short-eared Owls as an anti-predator adaptation because: (1) it minimizes the time predators have to locate nests, and (2) asynchronous dispersal can increase chances of reproductive success should a predator locate the nest in the latter stages of the

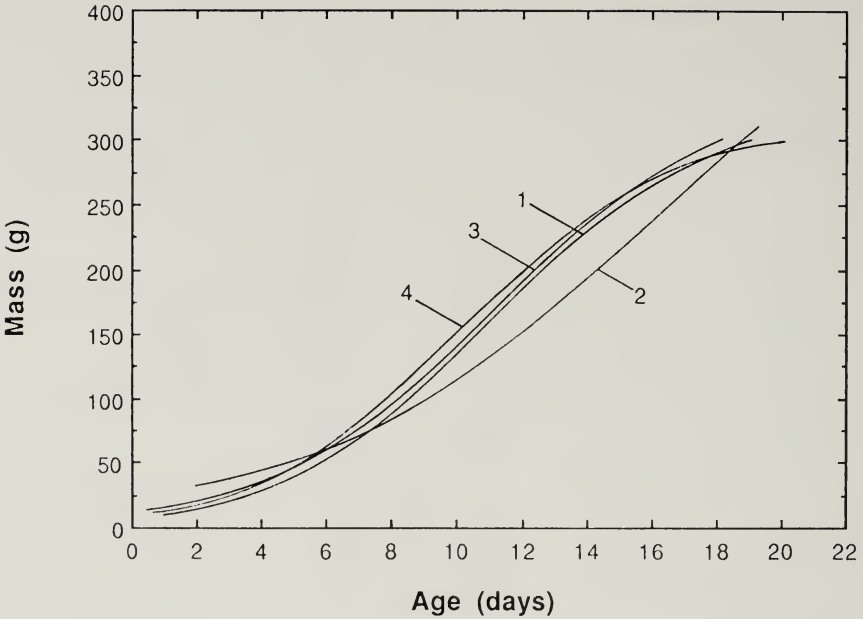

FIG. 2. Observed body masses and estimated median growth models for Short-eared Owl nests.

nesting period. Perhaps, pre-fledging dispersal also acts to reduce sibling brood cannibalism, but we are unsure if this is driven by natural selection or a by-product of pre-fledging dispersal. All cases of brood cannibalism in Short-eared Owls are reported to have occurred in the nest (Ingram 1962; D. Holt, unpubl. data).

Similar behaviors have been reported for the ground nesting Snowy Owl (*Nyctea scandiaca*) (Watson 1957, Taylor 1973) and Marsh Owl (*Asio capensis*) (Smith and Killick-Kendrick 1964). Ricklefs (1968) reported the Snowy Owl grows relatively more quickly than does the Barn Owl (*Tyto alba*) and Great Horned Owl (*Bubo virginianus*). He suggested that ground nesting Snowy Owls were subject to greater predation pressure than owls that nest above ground.

Wijnandts (1984) used the logistic model to compare growth for eleven species of owls. His growth constant (K) for the Short-eared Owl was 0.194, which is considerably lower than ours. Our Short-eared Owl growth constants were higher than those for any owls as computed by Wijnandts (1984) and buttress our argument that rapid growth for ground-nesting Short-eared Owls evolved as an anti-predator adaptation. Interestingly, Wijnandts' growth curves for ground nesting Snowy Owls (0.149) were much less than for Short-eared Owls. Ricklefs (1968) did state, however, that larger birds grow more slowly than smaller birds. Young Northern Eagle-Owls (*Bubo bubo*), whose nests are on the ground, disperse eight and 38 days before other Eagle-Owls that nest in trees or caves (Wijnandts 1984).

Clark (1975) provided the only other data describing Short-eared Owl nestling growth that we are aware of for North America. He reported data from three captive nestling Short-eared Owls. Two were hatched in an incubator, and a third was raised in captivity after

TABLE 2

DAILY INTERVALS AND ESTIMATED BODY MASS AT HATCHING AND BODY MASS INCREMENTS COMPUTED FROM THE MEDIAN MODELS

Intervals (days)	Estimated masses (g)		
	Start	End	Average daily change
Miacomet nest			
1–5	14.24	44.00	7.44
6–10	57.05	136.85	19.95
11–15	161.58	250.65	22.26
16–20	266.74	305.26	9.63
Cisco Beach nest			
1–5	26.60	53.05	6.61
6–10	62.58	115.82	13.31
11–15	133.17	216.01	20.71
16–20	238.76	326.85	22.02
Ram Pasture nest			
1–5	15.98	48.24	8.06
6–10	62.08	143.97	20.47
11–15	168.54	254.60	21.51
16–20	269.83	306.10	9.06
Golf Course Nest			
1–5	14.00	46.73	8.18
6–10	61.43	149.56	22.03
11–15	175.30	258.71	20.85
16–20	271.96	300.81	7.21

approximately 10 days of age. The two owls from the incubator weighed 16 and 18 g, respectively, at hatching and reached 210 and 230 g by approximately day 26. The owls grew slowly for the first eight to 10 days, and then rapidly from 10 to 20 days. The third owl grew rapidly from 7 to 18 days and then slowed. Its asymptotic weight was at approximately 385 g at age 27 days, its first flight day. The owl then fluctuated in weight between 360 g and 380 g from day 29 to 39 when data recording ceased. Clark's data are in agreement with our results.

Two of seven nestlings from the Golf Course nest lost body mass—the second oldest and the youngest. The mass loss of the youngest might be expected if food resources diminished or adults could not keep up with nestling needs. But why did the second oldest lose body mass? Lack (1954) stated that asynchronous hatching is an adaptation to food stress, with adults feeding the most active nestlings, usually the larger ones.

Gronlund and Mikkola (1969) reported mean hatching body mass for Short-eared Owls to be 15.4 g (range 14–17, N = 5), in Finland. They also reported that nestling Short-eared Owls leave their nests when 15 days old (range 14–18, N = 20). Watson (1972) reported that nestling Short-eared Owls in Scotland left their nest when 12 days old. Clark (1975) reported nestlings left when 13.6 days old (N = 6) in Manitoba, Canada. These pre-fledging

dispersal dates are similar among studies reported as well as the present one. Our estimates of fledging are also within the range reported by Urner (1923), 31–36 days, and by Clark (1975), 27 days, in the United States and by Witherby et al. (1940), 24–27 days, in Europe.

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DENVER W. HOLT, *Owl Research Institute, P.O. Box 8335, Missoula, Montana 59807*; SCOTT M. MELVIN, *Massachusetts Division of Fisheries and Wildlife, Westboro, Massachusetts 01581*; AND BRIAN STEELE, *Dept. of Mathematical Sciences, Univ. Montana, Missoula, Montana 59806.* *Received 22 Aug. 1991, accepted 10 Dec. 1991.*

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Frequency and timing of copulations in the Prairie Falcon.—Several authors (Birkhead et al. 1987; Møller 1987a, b; Birkhead and Lessells 1988) have commented on the high copulation frequencies in birds of prey compared to other avian taxa. However, there is a scarcity of observations on the copulatory behavior of birds of prey. Møller (1987a) described the copulation behavior of the Northern Goshawk (*Accipiter gentilis*), Birkhead and Lessells (1988) investigated copulatory behavior of the Osprey (*Pandion haliaetus*), and Sodhi (1991) that of the Merlin (*Falco columbarius*). Here, I describe the copulation frequency and timing of the Prairie Falcon (*F. mexicanus*), a large monogamous falcon of western North America (Palmer 1988).

Study area and methods.—From 1984–1987, I observed 52 breeding pairs of Prairie Falcons in the Snake River Birds of Prey Area (BOPA) and Reynolds Creek watershed in southwestern Idaho for 613 days (9085 h). A pair was considered breeding if eggs were laid (Steenhof 1987). The study area is part of the western intermountain sagebrush steppe, characterized by cold winters and hot, dry summers (West 1983). The vegetation is dominated by big sagebrush (*Artemisia tridentata*), winterfat (*Ceratoides lanata*), and shadscale (*Atriplex confertifolia*) associations (U.S. Dept. Interior 1979, West 1983). Observations started up to seven weeks prior to incubation and continued until young were 30–35 days old or the nesting attempt failed. Blinds placed at an average distance of 147 m (range = 70–250 m) from the aeries were used to make observations, aided by 10–45 × telescopes and 10 × 50 binoculars. Each nesting territory was observed, on average, once every six days by two observers, each on a half-day shift. I used an entire day as the sampling unit to avoid sampling problems related to daily behavioral cycles of the falcons (Altmann 1974). Observations started half an hour before sunrise and were terminated half an hour after sunset. Behavioral data were collected continuously, using focal animal sampling (Altmann 1974). Copulations were recorded as single events. I was not able to distinguish between successful (i.e., cloacal contact between mating birds) or unsuccessful copulations. Sex was determined by the larger size of the female and position of the falcons during copulations. Females solicited copulations and begged for food, unlike males. Falcons were not individually marked, but stylized drawings of each nesting falcon's facial pattern aided identification of individual birds. The establishment of stable territorial boundaries early in the nesting season (Ogden and Hornocker 1977, Sitter 1983, Holthuijzen, unpubl. data) and the general openness of the terrain further facilitated the distinction between nesting pairs and intruding falcons. The data presented here were collected as part of a larger behavioral study on Prairie Falcons. More details on the sampling procedure can be found in Holthuijzen (1990) and Holthuijzen et al. (1990).

Hatching dates were calculated by back-dating ages of young, using a photographic aging key (Moritsch 1983). Start of incubation was based on a 34-day incubation period (Burnham 1983). Observation days were categorized in six-day intervals based on the approximate stage of the nesting cycle relative to the female's estimated clutch completion date and labelled by midpoints (pre-incubation, N = 91 days of observation [DO]: days −51, −45, −39, −33, −27, −21, −15, −9, and −3; incubation, N = 267 DO: days 3, 9, 15, 21, 27,

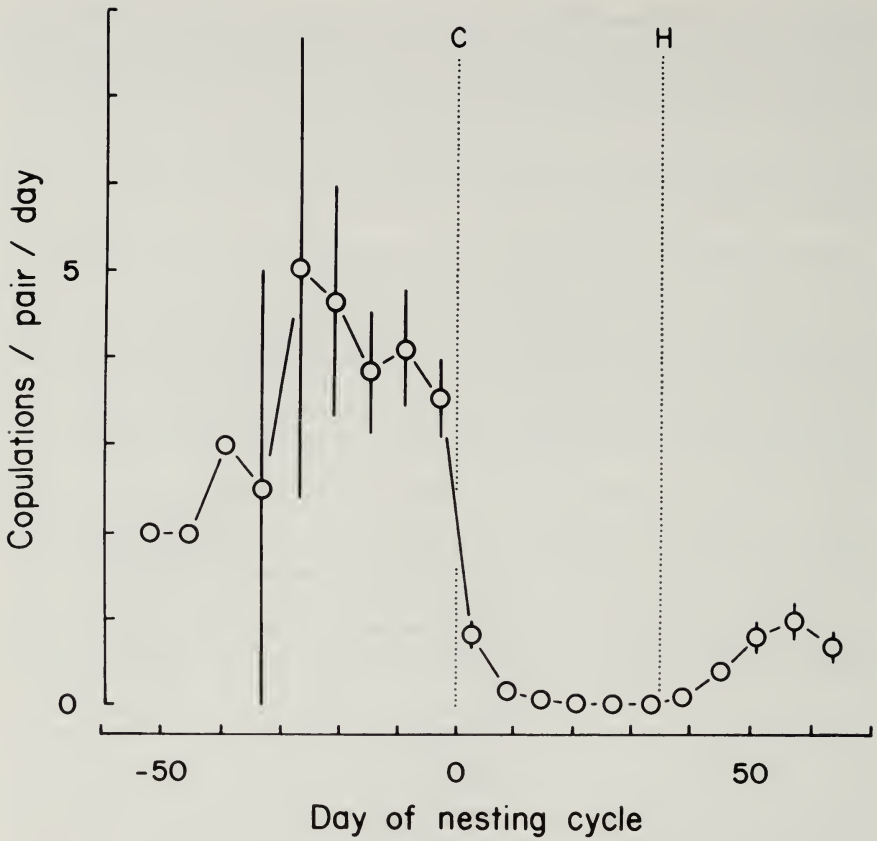

FIG. 1. Average number of copulations of Prairie Falcon pairs per day (±SE) during the nesting season (C = clutch completion, H = hatch).

and 33; and brood rearing, N = 255 DO: days 34, 39, 45, 51, 57, 63, and 69). Day 34 was included when falcons had newly hatched young (0–3 days).

The time of day when a behavior took place was standardized in hours after sunrise. Copulation frequency data were square root transformed (Sokal and Rohlf 1981). One-way analysis of variance (ANOVA) was used to determine differences in copulation frequency among nesting stages (copulations/day) and among hours of the day (copulations/h).

Results and discussion.—The total number of copulations over the 51-day pre-incubation period was estimated at 194 ± 15 (SE) copulations per clutch. On average, 28 ± 3 (SE) copulations per pair (N = 522 DO) occurred during incubation and brood rearing. The copulation frequency of the Prairie Falcon was high compared to the Osprey (59 copulations/clutch; Birkhead and Lessells 1988) and the Merlin (42 copulations/clutch; Sodhi 1991), but lower than the Northern Goshawk (500 copulations/clutch) (Møller 1987a), American Kestrel (*F. sparverius*; 690 copulations/clutch; Balgooyen 1976), and Eurasian Kestrel, *F. tinnunculus*; 374 copulations/clutch; T. Meijer in Birkhead and Lessells 1988).

None of the 553 observed copulations was identified as an extra-pair mating even though

the nesting densities of Prairie Falcons in the BOPA are the highest recorded for this species (U.S. Dept. Interior 1979). Birkhead and Lessells (1988) reported that EPC attempts occurred infrequently in Ospreys, but suggested that this may have been related to the low population density of Ospreys in the study area. Sodhi (1991) also recorded a small number of EPCs for the Merlin (3 of 41 copulations).

Copulations were observed at least 51 days prior to clutch completion, when falcons were already mated. Copulations peaked around 27 days before egg laying (Fig. 1) and remained high until clutch completion ($F = 29.59$, df = 21 and 591, $P = 0.0001$). Copulations averaged 3.8 ± 0.3 (SE) per day (N = 91 DO) during pre-incubation. Copulations then dropped off sharply and remained low throughout incubation (0.2 ± 0.04 [SE] per day [N = 267 DO]). During brood rearing the number of copulations per day increased again (0.6 ± 0.2 [SE] per day [N = 255 DO]). Most copulations (87.3%) took place during preincubation. To evaluate whether the copulation frequency peaked during the female's fertile period, I estimated the onset and duration of the female's fertile period (i.e., the period that sperm can be stored in the female's reproductive tract and remain viable up to oviposition of the last egg [Møller 1987a, Birkhead and Lessells 1988]). In captive, artificially inseminated Prairie Falcons sperm can remain viable for at least six days (Boyd et al. 1977). Fertilization of an ovum in these artificially inseminated females took place 50–60 hours prior to oviposition (Boyd et al. 1977). For an average clutch of 4–5 eggs in Prairie Falcons (U.S. Dept. of Interior 1979), I estimated the female's fertile period to be at least 12–14 days prior to clutch completion. Copulations were high 14 days before onset of the female's fertile period and remained high until clutch completion (Fig. 1).

During preincubation copulations per hour were highest in the first 2–3 hours after sunrise with a smaller peak in late afternoon to early evening ($F = 4.80$, df = 15 and 1408, $P = 0.0001$) (Fig. 2). During incubation copulation frequencies were similar among hours of the day ($F = 1.80$, df = 15 and 4176, $P = 0.03$). During brood rearing, however, copulation frequencies were higher during early mid-morning and early evening hours ($F = 2.77$, df = 15 and 3984, $P = 0.0003$).

To increase certainty of paternity, males can either guard their mates throughout the time that the females can be fertilized (Møller 1987c, Birkhead and Lessells 1988) or dilute sperm of possible competitors by frequent matings when they cannot guard the female (Birkhead et al. 1987). These predictions have been collectively referred to as the sperm competition hypothesis (Birkhead et al. 1987). Male Prairie Falcons provide for their mates (Holthuijzen 1990) and therefore, cannot guard the females continuously during the fertile period. In fact, Willoughby and Cade (1964) refer to the genus Falco as typical non-guarders. If sperm competition is an important factor determining copulation behavior, I would expect Prairie Falcons to have a high number of copulations per clutch, high copulation frequencies during the preincubation period, especially when the female is fertile, and optimal timing for fertilization during the day with peaks in the early morning and early evening (Birkhead et al. 1987, Birkhead and Lessells 1988). The results of this study are consistent with some of the predictions based on the sperm competition hypothesis. The number of copulations per clutch in Prairie Falcons is high compared to the number of copulations necessary for fertilization, a pre-requisite for the sperm competition hypothesis (Birkhead et al. 1987). Copulation frequencies in Prairie Falcons are high during preincubation, including the female's fertile period. Copulations also peaked in the early morning and late afternoon to early evening hours as predicted by the sperm competition hypothesis. There are significant deviations, however, in particular the absence of extra-pair copulations and no pronounced peak in copulatory activities during the female's fertile period. Several alternative explanations for high copulation frequencies in birds of prey have been proposed (Birkhead et al. 1987). Copulatory behavior during the preincubation period, before the female's fertile

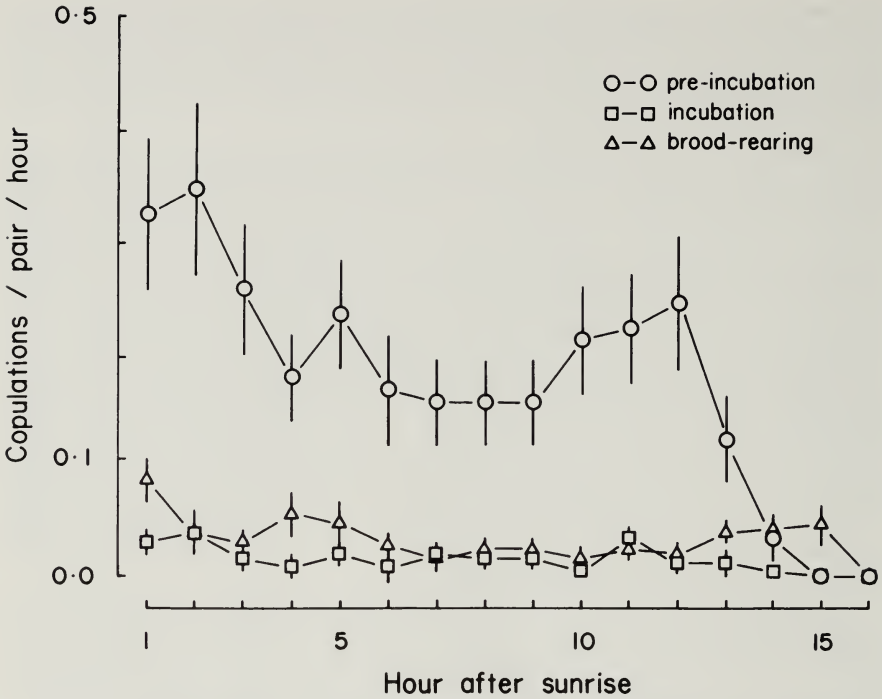

FIG. 2. Average number of copulations of Prairie Falcon pairs per hour (±SE) during the pre-incubation, incubation, and brood rearing stages.

period, can also be part of the mate assessment process, especially when the female solicits copulations (Birkhead et al. 1987), as is the case in Prairie Falcons. High copulation frequencies may be important in establishing the pairbond (Cade 1960, Newton 1979, Birkhead et al. 1987). Continued copulatory behavior after the female's fertile period suggests that this behavior may play an important role in maintaining the pairbond. In addition, increased copulatory activity during brood rearing may be related to a second nesting attempt. However, this explanation seems unlikely for Prairie Falcons nesting in the BOPA, because a second nesting attempt has never been recorded when the first one was successful (K. Steenhof, pers. comm.) (i.e., one or more young reached fledging age [Steenhof 1987]). No single hypothesis discussed here fully explains the observed copulatory behavior of Prairie Falcons. Maybe the copulatory behavior of the Prairie Falcon is driven by a combination of motivations. The data presented here cannot answer this question, but may be a starting point for further investigations.

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ANTHONIE M. A. HOLTHUIJZEN, *Idaho Power Co., Environmental Affairs Dept., P.O. Box 70, Boise, Idaho 83707.* *Received 1 Aug. 1991, accepted 20 Nov. 1991.*

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Pairbond persistence and "divorce" in Black-capped Chickadees.—Pairbond persistence over several years is common among parids including Black-capped Chickadees (*Parus atricapillus;* Odum 1942, Glase 1973); Carolina Chickadees (*P. carolinensis;* Brewer 1961, Dixon 1963); Mountain Chickadees (*P. gambeli;* Dixon 1965); and Plain Titmice (*P. inornatus;* Dixon 1949) in North America, and also in many European species, including the Great Tit (*P. major;* Hinde 1952) and others (reviewed in Perrins 1979). Occasionally, however, members of intact pairs may split up to form new alliances; Hinde (1952) and others have referred to this as "divorce." Among birds, divorce occurs when one member of an intact pair (two birds that bred together the last time breeding was possible) deserts its former mate to form a new pairbond with another bird; thus only birds that are at least one year old can be involved in divorce. Consequently, in birds such as Black-capped Chickadees, few, if any, birds with low winter rank can be involved in this process, since the vast majority of such birds (at least in most parid populations, including the chickadees in my study area) are less than one year old. In every divorce that I have observed, one bird moves and the other stays; I will consider the one that moves to be the bird that initiated the divorce.

This paper will examine all instances of divorce so far recorded in a small, color-banded population of Black-capped Chickadees in western Massachusetts, which I have been studying since the fall of 1979. During this time, the central winter population has varied from four to seven flocks, and the central breeding population, from 12 to 16 pairs (Smith 1988a, Smith 1991). This study population is not isolated physically from adjacent flocks or pairs, and for the purposes of the present paper, I also include data from banded members of peripheral chickadee groups.

Over the past ten years, I have recorded 15 instances of divorce among color-banded chickadees. During this same time period, 79 other intact pairs (just over 84%) remained together. Of the the 15 divorces, 10 were initiated by females and five by males. Three of these divorces occurred during winter; six occurred in spring (April and early May), and six occurred in late summer. All six of the spring divorces were early enough to permit breeding by the newly formed pair; by contrast, all of the summer divorces occurred too late for breeding to take place that year.

Fourteen of the 15 records involved clear rank increases for the divorce initiators (Table 1). Each male initiator went from beta to alpha male. Eight of the 10 female initiators went from second-ranked female to highest-ranked (in my study area, over the last 10 years, female winter rank has consistently reflected that of her mate; hence the top-ranked female is paired to the flock's alpha male). One female moved from third- to second-ranked female. Finally, one female (AlK KR; see Table 1) went from top-ranked female of a four-bird flock to top-ranked female of an eight-bird flock. Since most males rank above females during the nonbreeding season, a four-bird flock's highest-ranked female would rank above only one bird, whereas an eight-bird flock's highest female would rank above three other birds.

TABLE 1
DIVORCES: WINTER RANKS AND FLOCKS

Individual	Original rank[a]	New rank[a]	Birds from same or different flocks	If different, new pair joins flock of
Female initiators				
A1Y RB	2	1	same	—
A1O GK	2	1	same	—
A1R BB	2	1	same	—
A1R OB	2	1	same	—
A1Y YB	2	1	same	—
A1G BY	2	1	same	—
A1Y RO	2	1	same	—
A1K YY	3	2	same	—
A1R RK	2	1	different	female
A1K KR	1	1	different	(she died that summer)
Male initiators				
YG	2	1	same	—
A1R OO	2	1	same	—
A1G KO	2	1	same	—
A1K KK	2	1	same	—
A1R GY	2	1	different	female

[a] Within-sex rank in winter flock.

All but three new alliances involved members of the same flock (Table 1). The three between-flock alliances were all between members of two adjacent flocks. Somewhat surprisingly, of these three new pairs, the two that survived until flock formation (after first breeding together) both joined the female's home flock the following fall (Table 1). Both of these divorces were initiated in early spring.

All 15 divorces appeared to be triggered by the death of a high-ranked bird. The three winter records, all occurring before the winter of 1987–1988, were each instances of complex substitution: here a member of a flock's alpha pair dies, and is replaced by a member of the beta pair (the divorce), after which a winter floater settles into the beta pair, replacing the divorce initiator. Immediately after every winter divorce, each initiator not only seemed to associate extremely closely with its new mate, but also seemed actively to avoid the whereabouts of its former mate, which itself was associating very closely with a newly inserted winter floater (Smith 1984). From 1987–1988 on, however, the overall density of winter floaters in my study area has dropped considerably, and rapid replacements following winter mortality are now rare (Smith 1990). Therefore, most high-ranked chickadees that died during subsequent winters have not been replaced until the following spring, even when divorce was involved (see Smith 1990 for association index data). Hence the spring divorces include some cases of replacing high-ranked birds that have died four or five months earlier. Similarly, the summer records all appear to have occurred at the beginning of autumn flock formation, even if the death that triggered the divorce had occurred a month or two earlier.

Twice as many divorces were initiated by females as by males, although female mortality was not twice that of males during the same period. This is particularly true for winter and spring records. Looking only at mortality within the top-ranked pairs of each flock, male

TABLE 2
CHICKADEE DIVORCES: PAIRBOND PERSISTENCE

Sex of initiator	Year	Years with former mate	Years with new mate	Terminated by
F	1983	1+[a]	1	Her death
F	1983	1	1	His death
F	1985	1	2	His death
F	1986	1	2	Her death
F	1986	1	1	His death
F	1988	1	1.5	Her death
F	1988	2	1	His death
F	1989	2	2+[b]	(intact)
F	1989	1	2+[b]	(intact)
F	1991	1+[a]	1+[b]	(intact)
M	1981	2+[a]	1	Her death
M	1986	1	5.8	Her death
M	1988	1	2	His death
M	1990	1	1+[b]	(intact)
M	1991	2	1+[b]	(intact)

[a] Banded as an adult.
[b] Both still alive.

and female mortality from the end of August through the first week in May was identical over the ten years (16/66 for each sex), yet six females and only three males initiated divorces (winter and spring data combined). Nevertheless chi-square analysis reveals that these ratios do not differ significantly, possibly due to small sample sizes.

Chickadees that initiated one divorce were not likely to initiate another; indeed, each of the 15 divorces was initiated by a different bird, and every new alliance ended so far has been terminated by death, rather than by desertion (Table 2). Moreover, at least six of the new alliances persisted for at least two years, and one actually lasted for almost six years (Table 2).

As any bird grows older, it may passively increase its rank, due to increased age and/or mortality of other, higher-ranked birds. To examine whether the gains in rank of divorce initiators were any different from those their contemporaries gained through more passive means, I compared divorce initiators with non-initiators of the same sex, rank, flock size, and approximate age (I counted each bird only once). For winter divorces I examined final ranks at the end of that winter; for spring and summer divorces I compared initial rank in the previous winter with starting rank in the next winter's flocks. Fourteen of my initiators started at beta or below; all moved up in rank. By contrast, of 39 non-initiators starting at equivalent ranks, and surviving long enough to be assessed, only 12 increased their dominance, while 27 did not. Initiating a divorce was thus significantly more efficient at improving rank than was more passive behavior ($\chi^2 = 19.74$; 1 df).

Unfortunately, I do not have nest success data, so I cannot say how many, if any, of the spring and late summer divorces are correlated with poor nesting success. This is a possible alternative explanation, especially for late summer divorces. However, every one of the 15 divorces, including those initiated in late summer, resulted in the initiator ranking above more individuals than it had formerly. The more birds a chickadee ranks above at the

beginning of the nonbreeding season, the better its chances of avoiding ending the winter as the lowest-ranked bird of its sex (or indeed of the flock). This is particularly important for females, which rank below most males in the winter. Most (13/15) divorces involved moving from second- to top-ranked position within the bird's sex. For males, the advantages of becoming alpha in their flock are many. Some of the more obvious ones include preferential access to the best foraging sites, both in terms of food quality and safety against predators (see, for example, Ekman and Askenmo 1984, Desrochers 1989). Alpha males are also much more likely to be sought out for extra-pair copulations (Smith 1988b), and indeed, as the present paper shows, they are also less likely to be deserted through divorce than are beta males. Both members of a top-ranked pair are assured of obtaining a local breeding territory, which, in many parts of this species' geographic range, is not always possible for lower-ranking pairs (Smith 1967, 1984; Desrochers et al. 1988). Moreover, this territory is likely to be the best quality available (Smith 1976). Females that become paired to alpha males also gain a rather subtle but important advantage, documented by Ekman (1990) for Willow Tits (*Parus montanus*). He showed that females paired to dominant males were subject to aggression less often than expected, due to increased protection by their (alpha) mates. M. L. Withiam, D. Lemon, and C. P. L. Barkan (pers. comm.) have obtained similar data for Black-capped Chickadees.

Both sexes can initiate divorce. Even though twice as many females as males initiated divorces during a period when identical number of top-ranked vacancies occurred, this difference was not statistically significant. Future research is needed to see if there is truly no difference between males and females, or if, alternatively, females are actually more likely than males to seek out new, higher-ranking alliances.

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SUSAN M. SMITH, *Dept. of Biological Sciences, Mount Holyoke College, South Hadley, Massachusetts 01075.* *Received 11 Aug. 1991, accepted 12 Nov. 1991.*

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The effectiveness of Helmeted Guineafowl in the control of the deer tick, the vector of Lyme disease.—Lyme disease, a parasitic infection of increasing concern in the United States, is caused by a spirochete (*Borrelia burgdorferi*) spread by the deer tick (*Ixodes dammini,* Acarina, Ixodidae; Lane et al. 1991). A variety of measures for controlling the deer tick has been suggested, such as pesticides, burning, host eradication, or removal (Mather et al. 1987, Schulze et al. 1987, Wilson et al. 1988), but no single method has been demonstrated to be effective over a wide variety of habitats. Use of certain pesticides (Stone 1979) and host eradication, especially of the white-tailed deer (*Odocoileus virginianus,* Wilson et al. 1988), are not practical near areas of heavy human use such as playgrounds, school yards, and suburban housing developments.

The Helmeted Guineafowl (*Numida meleagris*) has been used as a "folk" defense against ticks acting as vectors for Lyme disease on Shelter Island, New York, and on the islands of Martha's Vineyard and Nantucket, Massachusetts. In Africa, this species eats a wide variety of arthropods (Skead 1962, Angus and Wilson 1964, Grafton 1971, Mentis et al. 1975) and gleans ticks from warthogs (*Phacochoerus aethiopicus;* Maclean 1984). In the United States, Crowe (unpubl. data) found ticks in the stomachs of three Helmeted Guineafowl in Nantucket.

Accordingly, we tested whether guineafowl might be useful in reducing tick populations in a series of controlled exclosure and enclosure experiments during September–November 1990 when adult deer ticks quest for large mammalian hosts (Daniels et al. 1989). Our experiments were performed at suburban sites in Easthampton, Suffolk County, New York, where free-ranging guineafowl had been introduced one year earlier to control high tick numbers, and in Islip, Suffolk County, New York, where guineafowl had not been present for ten years and tick populations previously seemed elevated (C. D. Webster, pers. comm.).

Although the deer tick is commonest in woodland (Maupin et al. 1991), we chose lawns because most human activity occurs on lawns and because people on lawns appear less likely to take precautions against ticks than when entering habitats such as woodlands (D. Duffy, pers. obs.). Lawns are also structurally more homogenous than woodland or hedgerow,

allowing a greater similarity of controls and cages. Finally, lawns appeared to be more or less uniformly used by foraging guineafowl, while our initial observations indicated greater small-scale variability in use of brush and woodland.

We placed ten exclosure cages at the Easthampton site at intervals of approximately 20 m along the edges of a 3.7 ha mowed meadow surrounded by hedgerow. Each exclosure was made of 10 cm mesh and was 1-m^3, with a mesh roof. A flock of 25–30 guineafowl fed freely over the meadow. To sample presence and numbers of ticks, we conducted one-min repeated drags of a 30 × 60 cm cloth over the ground within each exclosure at approximately one-week intervals from 15 October to 21 November 1990. Control samples were obtained in the same manner on the lawn immediately adjacent to each cage. Any ticks found were returned to the area sampled. We avoided sampling during rainy weather, on days following rain, or when ambient temperatures were below 10°C.

The Islip experimental landscape was lawn intermixed with second-growth woodland and unmaintained horticultural plantings. The enclosures were also placed on the edge of lawn immediately adjacent to denser vegetation around trees or shrubs. Four guineafowl were introduced into 2 × 2 m mesh cages on nine days between 22 October and 5 November 1990 (22, 24, 25, 31 October and 1–5 November). Cages were moved every day and birds were not put out during inclement weather or when the temperature was forecast to remain below 10°C. After removing the birds, we made three sequential one-minute sweeps using a 30 × 60 cm terry cloth on a one-m rope within each enclosure and then repeated the same procedure for two separate 2 × 2 m control patches immediately outside each enclosure, in the same habitat.

Following each one-min sweep, we recorded the presence and number of ticks and other arthropods on the drag. For analysis, we used the combined totals of the three counts for comparisons of frequency of occurrence between controls and experimental areas. In as much as we expected tick occurrence to be reduced in the presence of guineafowl, our tests were one-tailed (Sokal and Rohlf 1981).

The results of the exclosure experiment indicated a significantly higher probability of finding deer ticks within exclosures than outside ($G = 6.74$; $P = 0.01$). Ticks were present in eight of 50 samples of ten exclosures (7 samples had single ticks, 1 sample had 2) and in one of 50 controls. Similarly, the enclosure of guineafowl resulted in a reduced probability of encountering ticks within the four-m^2 cages, although the difference was not significant (Fisher Exact Probability Test, $P = 0.07$; no ticks were found in nine enclosures, while single ticks occurred in five of 18 outside controls). If the probabilities of the tests for enclosures and exclosures are combined as a test that the pattern of results could be due to chance alone (Sokal and Rohlf 1981), the resulting value ($-2 \Sigma \ln P = 14.8$) is greater than the χ^2 value of 13.82 at $P = 0.001$, suggesting a highly significant difference in tick presence in response to guineafowl activity.

At the Islip site, guineafowl also substantially reduced the occurrence of leaphoppers (Fisher Exact Probability Test, $P = 0.0195$; leafhoppers were present in three of nine enclosures and in 14 of 18 controls) and beetles in enclosures (Fisher Exact Probability Test, $P = 0.021$; beetles were present in one of nine enclosures and in 10 of 18 controls).

Our experiments suggest that predation by guineafowl reduced numbers of adult deer ticks on lawns adjacent to dense foliage at two sites on Long Island. Adult deer ticks have a 50–100% probability of being infected with the Lyme disease spirochete (Lane et al. 1991), so the presence of free-ranging guineafowl may help reduce the probability of contracting Lyme Disease from adult ticks on lawns and lawn edges. In addition, guineafowl reduced the presence of other arthropods, suggesting they may help reduce the need for chemical insecticides.

Our experiments tested only whether guineafowl could reduce adult tick populations. It

did not measure the density of birds needed for effective control of ticks. Other aspects also need to be investigated. For example, nymphal deer ticks present the greatest risk of transmitting Lyme disease to humans (Piesman et al. 1987), but they are smaller than adults and may not be captured as easily by guineafowl. Most deer ticks are found in woods or at the edges of woods (Maupin et al. 1991), habitats used by foraging guineafowl to a lesser extent than lawns (D. Duffy, pers. obs.). Are guineafowl effective predators of ticks in less open habitats?

Guineafowl are inexpensive compared to many pesticide treatments and present less potential for direct environmental damage. On the other hand, guineafowl have several drawbacks that may make them unsuitable in some situations. They are noisy and may be objectionable to human neighbors. Their droppings, while serving as a fertilizer, may be unpleasant if the lawn is used for human recreation. On the other hand, the droppings may discourage some human behaviors, such as sitting on the ground, that increase the risk of contracting Lyme Disease. Finally, the birds are sometimes vulnerable to predation by feral or free-ranging dogs (C. Brinkley, pers. obs.), so that a fenced yard may be needed to reduce flock mortality.

Guineafowl may be most appropriate as one means of controlling ticks in low-density housing areas and in public parks and school yards where their noise is unlikely to be a problem and where custodial care is available for the flock. Guineafowl alone should not be relied on for the complete control of deer ticks, but rather should be used as one of a suite of methods such as tick repellents, judicious use of acaricides, and habitat modification to reduce the risk of Lyme disease.

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David Cameron Duffy, *Lyme Disease Research Project, Box 1029, Shelter Island, New York 11964;* Randall Downer, *Applied Biomathematics, 100 N. Country Road, Setauket, New York 11733;* and Christie Brinkley, *% Gelfand, Rennnert, and Feldman, 6 E. 43 Street, New York, New York 10017.* *Received 22 Oct. 1991, accepted 10 Jan. 1992.*

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Song repertoires of the White-browed Blackbird.—The vocal behavior of the White-browed Blackbird (*Leistes superciliaris*), a locally common species in grassland and pastures of Argentina, Uruguay, Paraguay, Bolivia, southeastern Brazil, and Peru has been studied poorly. The taxonomic status of *L. superciliaris* is uncertain, as the bird appears to form a superspecies with the Red-breasted Blackbird (*L. militaris*; Short 1975). The latter replaces *L. superciliaris* northward, and they occupy open areas in the Amazon river region from Peru to the state of Para in northern Brazil (Meyer de Schauensee 1982). Like most other species in this genus, *L. superciliaris* is generally terrestrial, gregarious during the nonbreeding season, and sexually dimorphic in coloration. In the Argentine pampas, the breeding season lasts from September to February, and it is during this period that males sing. Here, I describe in detail the flight song (FS) and the perched song (PS) of *L. superciliaris* in the Argentine pampas. Also, I present evidence on the sharing of FS features among neighboring males.

Methods.—From September to December 1989, songs from 23 adults of *L. superciliaris* were recorded at the University of Luján Campus, Partido of Luján, northeast Buenos Aires Province, Argentina. Eight other neighboring males were recorded on 12 October 1990. Luján Campus is a typical agro-ecosystem with a dominant open herbaceous vegetation and several scattered introduced tree species (e.g., *Eucalyptus* sp.). Although birds were not banded, the chance of recording the same subject twice in the same day was negligible because simultaneous observation of several territorial neighbor males was possible. In addition, to avoid including the effect of possible song variation during the study period, I restricted the analysis of syllable sharing to those small neighborhoods where all males were recorded on the same day.

Recordings were made with a Uher 4000 Report-L at a speed of 9.5 cm/sec, using a directional hypercardioid Lec 970 LEEA microphone. Only best quality recordings were sonographed (total = 196 songs, ranging from 1 to 16 songs/individual) using a Kay Electric

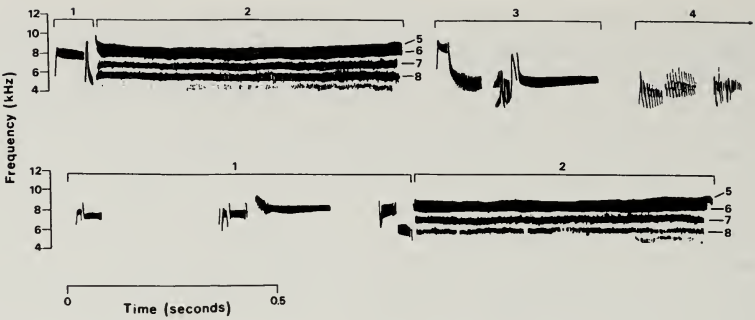


FIG. 1. Sonograms of the flight song (top) and perched song (bottom) of *L. superciliaris*. Parts of the respective vocalizations are as follows: (1) introductory phrase; (2) harsh central note; (3) ending phrase; (4) "chirp" notes; (5) and (6) principal bands; (7) and (8) first and second accessory bands.

Sonagraph 7029-A, set for wide band filters and the 160–16000 Hz frequency range. The terminology used to describe song follows Kroodsma (1974), except that I define syllable as a note or group of notes that can be recognized as a unit in the song of the same or different individuals. On each sonogram, I measured total duration, and maximum and minimum frequencies of the complete song and of each of the song phrases. For the quantitative description of the song, only the clearest sonogram of each song type of each individual was considered. Additionally, a catalog of the FS syllable types was compiled, and the sharing of syllable types among males was analyzed employing the isogloss method (for a detailed description of this method and its application in birds, see Mundinger 1982). Due to the small and scattered distribution of males whose PS were recorded, the isogloss analysis of the PS could not be performed.

Results.—The song repertoire of the White-browed Blackbird is composed of the FS and the PS, differing both in their acoustical structure and associated behavior (Fig. 1). The FS is composed of three phrases: a brief ($\bar{x}$ = 137 msec, SD = 79 msec, N = 31) introductory series of one to three syllables, a long ($\bar{x}$ = 633 msec, SD = 90 msec, N = 31) harsh central note, and a final phrase (lasting a mean of 381 msec, SD = 154 msec, N = 31) of two to four syllables. Next to this last phrase there is a series of complex "chirp" syllables.

The FS is broadcasted at the top (6–12 m of height) and during the descending part of a flight display. This typically consists of an oblique ascending flight leading into a brief and fast ascent in an almost vertical trajectory followed by a short drop and a descending flight. Only rarely was the FS sung at the top of a tree (one of the 31 subjects [3.2%] studied) or during a "multipeak flight display" (two subjects [6.4%]). In this last case, the flight display consisted of two or three successive peaks, each one accompanied by an utterance of a FS.

The perched song (Fig. 1) is always sung from a perch, usually near the ground (up to 1.5 m of height). In contrast to the FS, the PS lacks the final phrase and "chirp" syllables. For seven males in which both PS and FS were tape-recorded, the PS introductory phrase was significantly longer ($\bar{x}$ = 826 msec, SD = 185) and was more complex ($\bar{x}$ = 5.29 syllables, SD = 1.11 syllables) than the FS' counterparts ($\bar{x}$ = 162 msec, SD = 84; $\bar{x}$ = 2.43 syllables, SD = 0.51 syllables; Wilcoxon matched pair sign-ranked tests t = 0, df = 7, $P < 0.02$, two-tailed). In addition, the harsh central note was longer in the PS ($\bar{x}$ = 746 msec, SD = 133 msec) than in the FS ($\bar{x}$ = 645 msec, SD = 102 msec), but this difference was not statistically significant (t = 3.5, df = 7, $P > 0.05$). FS and PS did not differ in frequency, both ranging between 2.8 and 9.5 kHz ($t \geq 9$, df = 7, $P > 0.05$).

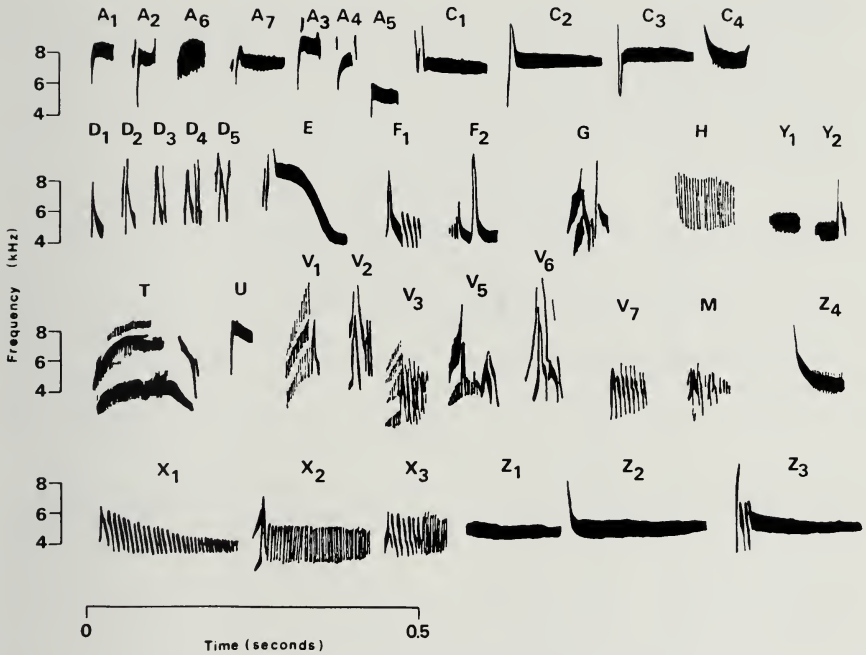

A1 A2 A6 A7 A3 A4 A5 C1 C2 C3 C4
D1 D2 D3 D4 D5 E F1 F2 G H Y1 Y2
T U V1 V2 V3 V5 V6 V7 M Z4
X1 X2 X3 Z1 Z2 Z3
8
6
4
Frequency (kHz)
0
0.5
Time (seconds)

FIG. 2. Catalog of syllable types and minor variants found in the introduction and ending phrase of the flight song of *L. superciliaris*. Syllable types are identified with letters and minor variants within each category with numbers. Syllables A to H are introductory syllables, and the rest correspond to the ending phrase. Syllables V_7 and M are the "chirp" notes that usually follow the ending phrase.

The complex structure of the harsh central note (HCN) includes a wide range of frequencies, from 4 to 9.5 kHz, but energy is mostly concentrated in a number of narrow bands of steady frequency. Typically, there are two "principal" bands of high frequency and amplitude, and two "accessory" bands of low frequency and amplitude (Fig. 1). The two principal bands contact in the frequency axis, and they are separated at regular intervals from the accessory bands. The number of bands of emphasized frequency also exhibit some degree of inter-individual variation. Three of the 31 subjects (9.7%) studied had only one principal band, and only one of them (3.2%) also had one accessory band. In addition, in at least one individual, the HCN contained more than two accessory bands. Although these bands of emphasized frequency could represent harmonic tones of a low fundamental, they may also be the product of a two voice phenomenon (Gaunt 1983). Unfortunately, on the basis of sonograms alone, it is impossible to determine in this case the exact nature of the HCN.

Excluding the HCN, 39 FS syllable types and variants were defined (Fig. 2). Table 1 shows that individuals differ in the number, type, and sequence of syllables employed in FS.

To illustrate the geographic distribution of the syllable types and variants, isoglosses were drawn. Fig. 3 depicts this analysis in two song neighborhoods. Neighboring males usually share the same syllabic variant, and there is concordance among the distribution of the different variants. This concordance is reflected by the existence of small groups of neighboring males (of up to three or four individuals) having almost identical song patterns (e.g.,

TABLE 1

SEQUENCE OF SYLLABLE TYPES IN THE FLIGHT SONG OF WHITE-BROWED BLACKBIRDS

Bird syllable sequence[a]	Bird syllable sequence	Bird syllable sequence
S_1[b] C_4F_1H-HCN-V_6Z_1	S_{11} HA_1D_1-HCN-X_3Z_1	S_{21} EA_1D_3-HCN-V_3Z_1
S_2 D_2-HCN-$Y_2V_3UX_2$	S_{12} A_3D_4-HCN-V_3Z_3	S_{22} EA_1D_3-HCN-V_3Z_1
S_3 $C_1A_2A_5$-HCN-$Y_1V_3Z_1$	S_{13} A_1D_4-HCN-V_3Z_3	S_{23} A_1G-HCN-$TV_3X_3Z_1$
S_4 A_6D_3-HCN-$V_6Z_1X_1$	S_{14} A_2G-HCN-$TV_3X_3Z_2$	S_{24} A_1D_1-HCN-$UZ_4V_5Z_2$
S_5 A_6D_3-HCN-$V_6Z_1X_1$	S_{15} A_2F_2-HCN-V_2Z_2	S_{25} A_1D_4-HCN-V_3Z_3
S_6 ED_2-HCN-V_5Z_1	S_{16} $A_4C_2D_5$-HCN-$Y_1V_1Z_2X_2$	S_{26} A_1D_1-HCN-$UZ_4V_5Z_2$
S_7 $A_4C_3D_5$-HCN-$Y_1V_1Z_2X_2$	S_{17} ED_2-HCN-V_5Z_1	S_{27} A_1D_4-HCN-V_3Z_3
S_8 A_3D_4-HCN-V_3Z_3	S_{18} $A_4C_2D_5$-HCN-$Y_1V_1Z_2X_2$	S_{28} A_1D_4-HCN-V_3Z_3
S_9 A_1D_3-HCN-V_3Z_3	S_{19} A_1D_1-HCN-UZ_4Z_2	S_{29} A_1D_3-HCN-V_5Z_1
S_{10} A_1D_4-HCN-V_3Z_3	S_{20} A_6D_3-HCN-$V_6Z_1X_1$	S_{30} C_4F_1H-HCN-V_6Z_1
		S_{31} A_1G-HCN-$TV_3X_3Z_1$

[a] Syllable types as indicated in Fig. 2. Hyphens separate flight song phrases.
[b] Subjects S_1 to S_{23} recorded during 1989, and S_{24} to S_{31} recorded during 1990.

subjects S_{16} and S_{18}; S_{24} and S_{26}; S_{25}, S_{27} and S_{28}; in Fig. 3). A similar situation has been found in the House Finch (*Carpodacus mexicanus*) by Bitterbaum and Baptista (1979).

Discussion.—This study shows that the White-browed Blackbird has a repertoire of two song types, the FS and PS. These types differ in acoustical structure and associated behavior. The FS is more complex than the PS and has an ending phrase followed by a series of chirp notes. The PS lacks this end phrase and chirp notes, and it has an introduction longer than the FS. Besides, the PS is almost always broadcasted at a low perch, while the FS is emitted during the descendent part of a conspicuous flight display.

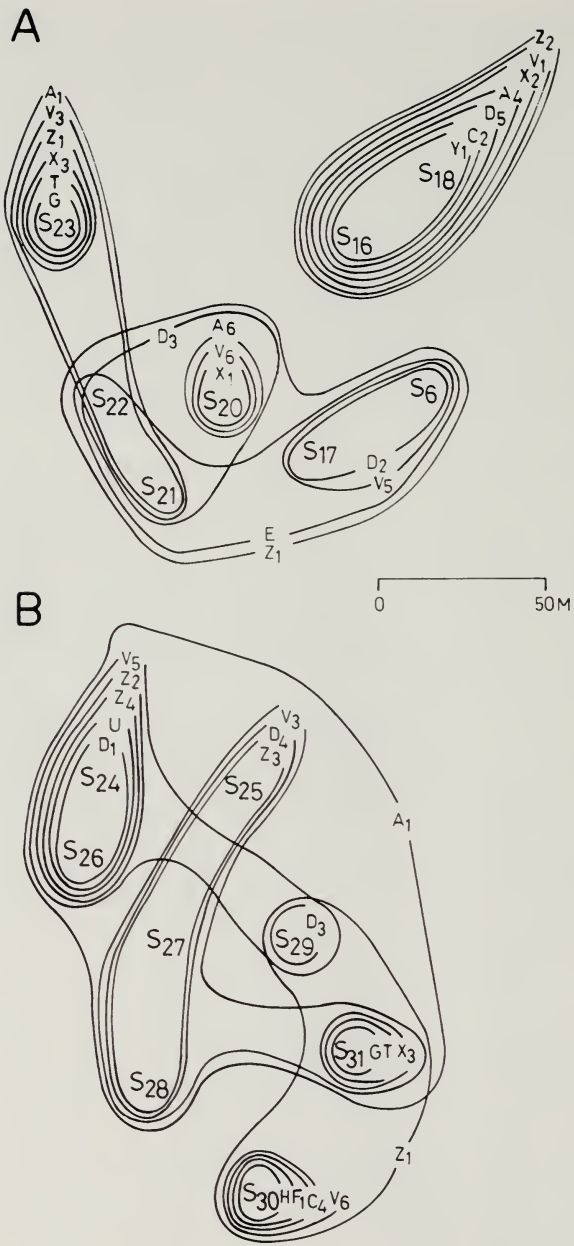
Although each male has distinctive flight and perched songs, it is possible to establish the existence of syllable sharing among neighboring males. Syllable and song sharing has been reported in a variety of Icterids: Eastern and Western Meadowlarks (*Sturnella magna* and *S. neglecta*; Lanyon 1957); Yellow-rumped Cacique (*Cacicus cela*; Feekes 1977, Trainer 1989); Red-winged Blackbird (*Agelaius phoeniceus*; Marler et al. 1972); Bobolink (*Dolichonyx oryzivorus*; Avery and Oring 1977); and Brown-headed Cowbird (*Molothrus ater*; Dufty 1985), but the presence of FS dialects (i.e., song variants characteristic of local groups of males, separated by well defined boundaries) has only been described for the latter (see "flight whistle" dialects in Rothstein and Fleischer [1987]).

Whether FS sharing among neighboring White-browed Blackbird males represents a dialect system is a matter of debate, but if true, it is clear that it differs from the flight whistle dialects in the Brown-headed Cowbird. These differences include the number of individuals sharing the "dialect" and its temporal stability, both features being smaller in the former than in the latter. During 1990, I looked for song neighborhood "A" (Fig. 3), but this area was found empty, as well as many other sites occupied by this species during 1989. Despite the lack of temporal stability of song neighborhoods, the clumped distribution of syllables and song patterns in *L. superciliaris* suggests that vocal imitation among neighboring males plays a role in song development.

Why does *L. superciliaris* fly during singing? In open habitats, temperature and wind gradients could refract sound, creating a shadow zone for the horizontal propagation of sound above the ground (Morton 1975, Wiley and Richards 1982). Singing at a greater height increases the active space of the song (i.e., distance from the source over which signal amplitude remains above the detection threshold of potential receivers), since the distance along the ground to the shadow zone increases with the square root of the singer's height (Wiley and Richards 1982). In addition, singing at a greater height also has the advantage of increasing the bird's visual conspicuousness and minimizing the acoustical interference generated by orthopteran songs emitted on or near the ground. In the absence of elevated song perches, it could be useful to fly during singing.

The presence of flight song displays is widespread among bird species living in open habitats (Armstrong 1963, Morton 1975, Miller 1983). The occurrence of flight display varies among *Leistes* and *Sturnella* species, indicating a possible relationship between the lack of elevated song perches and the presence of this behavior. Thus, while *L. superciliaris, L. militaris,* Lesser Red-breasted and Peruvian Red-breasted Meadowlarks (*S. defilippi* and *S. bellicosa*) live in open grasslands and exhibit a flight display during which the FS is emitted, Long-tailed Meadowlarks (*S. loyca*) which inhabit shrub areas with abundance of song perches, lacks a flight display (Hudson 1920, Gochfeld 1979).

Why do the flight song and perch song of the White-browed Blackbird differ in structure? In addition to the possible differences in their communicative function, it is tempting to relate the structural differences between the PS and FS to those existing in the acoustical properties of the pathways in which they are broadcasted. Shiovitz (1975) and Richards (1981) suggested that song introduction could function as an alerting element, thus facilitating the detection of the biologically significant part of the signal by removing the uncertainty


A
A1
V3
Z1
X3
T
G
S23
Z2
V1
X2
A4
D5
C2
Y1
S18
S16
D3
A6
V6
X1
S20
S22
S6
S17
D2
V5
S21
E
Z1
0
50M
B
V5
Z2
Z4
U
D1
S24
V3
D4
Z3
S25
A1
S26
S27
D3
S29
S31
GT X3
S28
Z1
S30
HF1
C4
V6

about its time of arrival. Interestingly, the PS has a longer and comparatively more complex introduction than the FS, just as would be expected for a signal emitted in a heavily interfered channel. In addition to the song shadows produced by the thermal and wind gradient, the acoustical interference of orthopteran songs mainly affects PS, because it is sung from low perches near the ground. These facts could make necessary the use of a long tonal introduction which could result in an improvement of receiver detection.

Even though the song introduction could function as an alerting element, the structural differences between the flight and perched song introductions could be explained in a different way. The visual conspicuousness of the ascending flight, previous to the FS start, could alert receivers about the incoming acoustical signal, avoiding the need to include additional alerting elements in the FS introduction.

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Fig. 3. Isogloss analysis of the *L. superciliaris* FS. Capital letters with subscripts indicate the syllable type and variant mapped by the isogloss (following the nomenclature of Fig. 2). The letter "S" with subscript identify the position of different males. Neighborhoods "A" and "B" were recorded during 1989 and 1990, respectively.

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PABLO LUIS TUBARO, *Laboratorio de Fisiología del Comportamiento. Instituto de Biología y Medicina Experimental. Obligado 2490. 1428—Buenos Aires, Argentina.* *Received 3 June 1991, accepted 12 Oct. 1991.*

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Social organization in Snow Geese: family size and individual behavior.—Great importance has been given to the family and its role in goose and swan societies (Raveling 1970, Prevett and MacInness 1980, Scott 1980, Lamprecht 1986, Black and Owen 1989). The social hierarchy of wild geese may be based on the family (or social unit) rather than on the individual (Boyd 1953, Hanson 1953, Raveling 1970, Black and Owen 1989), and individual ranks may not be independent from each other. For example, if individual "A" obtains rank 1, no other individual can obtain that rank. Moreover, the ranks of unit members are dependent on each other, that is, a juvenile cannot obtain a higher rank than its father or mother. Therefore, if a family gander has a low rank, all the members of its family have low ranks. The assertion that the behavior and characteristics of the individuals comprising these social units is unimportant compared to the social unit has not been unequivocally demonstrated, however. Although it was first thought that the number of individuals in a unit was the major determinant of rank (Boyd 1953, Hanson 1953, Raveling 1970, Black and Owen 1989), Lamprecht (1986) found in Bar-headed Geese (*Anser indicus*) that the rank of a family is determined mainly or solely by the behavior of the gander. Furthermore, events happening during hierarchy formation may also influence the dominance status eventually attained by a family.

We determined the relative importance of the nature and size of the social unit on the one hand, and the characteristics and behavior of individual birds composing these units, on the other, in the establishment and maintenance of the nested hierarchy in Greater Snow Geese (*Chen caerulescens atlantica*). The present study was conducted at La Pocatière, 100 km northeast of Québec city, Canada, between May and August 1988. Geese were cannon-netted, sexed, and fitted with numbered plastic neck collars. Age was determined as: (1)

juvenile; <one-year-old (grey), and (2) adult-plumaged; >one-year-old (white). All 138 birds of a single catch were released in a covered enclosure and observed from a blind. Groups of related individuals, such as families and pairs, were determined by the tendencies of certain individuals to associate. Groupings were often confirmed by the performance of the triumph ceremony by members of a unit (Fischer 1965). Two similar captive flocks of 18 geese each were then formed. Each group was composed of nine social units as follows: a family of five (i.e., three juveniles and two adults), a family of three (two adults and one juvenile); a pair; two single, unrelated adult-plumaged birds (one male and one female), three single, unrelated juveniles, and a group of three juveniles without parents (JWP). The geese were weighed, and tarsus, culmen, and fat thickness on the breast, abdomen, and thigh were measured. Total fat reserves were calculated using Gauthier and Bédard's technique (1985). Primaries of both wings were clipped to render the geese flightless. Death of an adult female between capture and the beginning of the observation reduced the size of group B to 17. Two groups of 18 geese were released in adjacent enclosures of 20 × 20 m, separated visually. The observations were made from an elevated (5 m) blind located between the two enclosures, so that the two groups could be observed simultaneously by two observers. Geese were observed 6 h/day, beginning at sunrise, and continuous behavior sampling was used. Agonistic interactions were recorded on tape and transferred to computer. For each agonistic interaction, the identity of the opponents, their role (attacker or victim), their success (winner or loser) and the intensity of agonistic behavior were recorded. Intensity was divided into five levels (modified from Black and Owen 1987). The rank orders of individuals and social units were determined by calculating the percentage success (wins/total encounters × 100) (Black and Owen 1989). We also calculated an index of dominance (number subdominant/total number of geese × 100) (Lamprecht 1986) from a dominance matrix. The matrix also yielded Landau's linearity index (from 0, no linearity, to 1, perfect linearity) which enabled us to test for the permanence of the hierarchies (Landau 1951). The relationships between morphological measurements and rank were assessed within each group using Spearman rank correlations. SAS utility system was used throughout. We found that all members of a unit had adjacent ranks, and thus, had relatively similar dominance indices (Table 1) except for the pair of group A. This pair was formed of a successful and highly ranked male and of a submissive low ranked female (Table 1). We found that in group B, the large family dominated the small one, but in group A the large family was dominated by the small one and even by the male of the pair (Table 2). Furthermore, in group B, according to the dominance index, the pair was dominated by the lone adult male, although it had a lower percentage success (Table 2). Otherwise, single adults ranked behind pairs and juveniles (single and JWP) ranked lowest (Tables 1 and 2). Using the dominance index of each individual (Table 1) we tested if some of their morphological characters were associated with their rank. We found significant correlations between weight and rank and total fat reserve and rank for group B ($r_s = -0.72$ and -0.5: $P < 0.05$ df = 17 for weight and total fat reserves, respectively). Our results, as do those of Turcotte (1987), show that large families did not always dominate small ones and pairs. However, they are consistent with published work in showing that families and pairs dominate lone adults (Boyd 1953, Hanson 1953, Raveling 1970, Scott 1980, Lamprecht 1986, Turcotte 1987, Black and Owen 1989). If, as Lamprecht (1986) stated, the rank of a unit is mostly determined by the characteristics and behavior of the gander, the low aggressiveness of the males may explain the low ranks of the large family and of the pair. In group A, the male of the dominant unit, the family of three, was very aggressive (1469 attacks initiated) while that of the large family, which ranked third, was not (359 attacks initiated). In group B, according to the dominance index, the pair was dominated by the single adult male. In both instances, where the unit had a rank lower than expected, both males were meek while the females were attacking

TABLE 1

INDIVIDUAL RANKS IN TWO GROUPS OF CAPTIVE GREATER SNOW GEESE OBTAINED USING % OF SUCCESS (RANK 1) AND DOMINANCE INDEX (RANK 2)[a]

Status	Sex	Age	No. attacks	% Success	Rank 1	Dominance index	Rank 2
				Group A			
F3	M	A	1469	99.8	1	100	1
F3	M	J	1106	98.1	2	88.2	4
F3	F	A	1198	97.6	3	94.1	3
F5	F	A	688	71.1	4	64.7	7
P	M	A	511	70.1	5	94.1	2
F5	M	J	390	54.1	6	52.9	9
F5	M	A	359	52.4	7	76.5	5
F5	F	J	339	51.6	8	47.1	10
F5	M	J	309	45.1	9	58.8	8
P	F	A	212	42.3	10	64.7	6
SA	M	A	504	38.4	11	35.0	12
SA	F	A	273	32.9	12	35.0	11
JWP	F	J	242	27.8	13	18.0	15
JWP	F	J	122	16.7	14	24.0	14
JWP	M	J	120	16.0	15	29.0	13
SJ	M	J	126	15.1	16	12.0	16
SJ	M	J	69	4.9	17	12.0	17
SJ	F	J	0	0	18	0	18
				Group B			
F5	M	A	1857	100	1	100	1
F5	M	J	1830	100	2	87.5	3
F5	F	J	1511	99.5	3	81.3	4
F5	F	J	1298	99.2	4	75.0	5
F5	F	A	1468	98.7	5	93.8	2
F3	F	A	775	50.1	6	62.5	7
F3	M	J	702	49.2	7	56.3	8
F3	M	A	619	47.3	8	68.8	6
P	F	A	802	42.2	9	37.5	11
SJ	M	J	866	37.7	10	25.0	13
P	M	A	607	36.2	11	43.8	10
SA	M	A	518	33.5	12	50.0	9
SJ	M	J	398	26.9	13	31.0	12
JWP	M	J	67	4.8	14	6.3	16
JWP	F	J	64	4.6	15	12.5	15
JWP	M	J	59	3.6	16	18.8	14
SJ	F	J	27	2.0	17	0	17

[a] F5 = family of 5, F3 = family of 3, P = pair, SA = single adult, SJ = single juvenile, JWP = juvenile without parents, F = female, M = male, A = adult, J = juvenile.

TABLE 2

RANKS OF SOCIAL UNITS IN TWO GROUPS OF CAPTIVE GREATER SNOW GEESE OBTAINED USING % OF SUCCESS (RANK 1) AND DOMINANCE INDEX (RANK 2)

Status	% Success	Rank 1	Dominance index	Rank 2
		Group A		
Family of five	52.6	3	60	3
Family of three	98.6	1	100	1
Pair	59.1	2	80	2
JWP	20.6	5	20	5
Single adult	36.3	4	40	4
Single juvenile	6.9	6	0	6
		Group B		
Family of five	99.5	1	100	1
Family of three	48.9	2	80	2
Pair	39.4	3	40	4
JWP	4.3	6	0	6
Single adult	33.5	4	60	3
Single juvenile	25.1	5	20	5

more often (688 attacks for the female of the family of five against 359 for the male and 802 attacks for the female of the pair against 607 for the male, Table 1). Our results also suggest that the aggressiveness of the male, based on the number of interactions initiated, plays an important role in the rank of its unit and that unit size may not be as important as previously thought for the determination of rank. The lack of aggressiveness shown by some males may result in looser family bonds (Raveling 1970) and, consequently, in lower rank for its unit. However, our results do not show that aggressiveness of males is related to family size (Raveling 1970). The male of the family of five (in group A) was not very aggressive, although it had three juveniles, whereas the male of the family of three demonstrated high aggressiveness. Our results rather confirm that there is a large range of variation in aggressiveness by individual ganders regardless of unit size. Our results show that females and juveniles rank higher when they belong to a family or a pair than when they are alone. We might think that, when in family, females and juveniles acquire the rank of the male. They may acquire this higher rank because of the strong family cohesion and the help and motivation provided by the male in encounters, which allows them to be recognized by the victim or a potential attacker as being members of that male's family. However, the male may also have a lower rank when he is not with his family (Lamprecht 1986). Although Raveling (1970) mentioned the importance of the male in the success in rank order of a unit, all authors, with the exception of Lamprecht (1986), concluded that the rank of a unit is dependent upon unit size (Boyd 1953, Hanson 1953, Raveling 1970). Therefore, it would be interesting to test for the effect of the male on the rank of its unit. This could be done by comparing the ranks of a group of ganders (isolated from their family units) and those of their families (including the gander). The results from the correlation analyses indicate that tarsus and culmen length, which were used as predictors of body size, are not associated with rank. These results agree with those of Lamprecht (1986) who found

only low correlations between these factors and dominance. The relationship between weight and rank is highly variable. We found a significant correlation in group B but not in group A. The greater variability of weight in group B (c.v. = 11 and 15 for group A and B, respectively) can explain these results. This is consistent with published results, as some investigators found significant correlations (Scott 1980, Black and Owen 1989) while others found none (Lamprecht 1986). Since total fat reserve is partly dependent upon body mass, it comes as no surprise that it should also relate to rank. Thus, there is some evidence from our results that rank determination and dominance in Greater Snow Geese units is a summation of many factors, of which male aggressiveness seems to be uppermost. However, further experimentation needs to be done to evaluate the importance of the family on dominance.

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Sylvie Cloutier and Jean Bédard, *Départ. de Biologie, Faculté des sciences et de génie, Univ. Laval, Ste-Foy, Québec, G1K 7P4, Canada.* (Present address SC: *Départ. de Psychologie, Univ. du Québec à Montréal, c.p. 8888, Montréal, Québec, H3C 3P8, Canada*). *Received 22 Jan. 1991, accepted 1 Oct. 1991.*

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Drinking, vigilance, and group size in White-tipped Doves and Common Ground-Doves in Costa Rica.—Animals are vigilant for predators because it reduces their chance of being preyed on, but vigilance is costly because it takes time away from other important activities (Bertram 1980, Krebs and Davies 1987, Cords 1990). Researchers have directed their attention primarily toward vigilance while potential prey are foraging (Page and Whitacre 1975, Caracao 1979, Hart and Lendrem 1984). Such vigilance decreases risk of predation (Lazarus 1978, 1979), kleptoparasitism (Thompson and Lendrem 1985), and human disturbance (Knight and Knight 1986). In general, vigilance of individuals decreases with group size (Lazarus 1979, Abramson 1979, Caracao 1979), indicating that this chore can be shared among group members.

Study area and methods.—I examined vigilance behavior of White-tipped Doves (*Leptotila verreauxi*) and Common (*Columbina passerina*) Ground-Doves at Palo Verde National Wildlife Refuge in Northwestern Costa Rica in March 1990. Palo Verde is a tropical lowland deciduous forest adjacent to marshes and the Tempisque River. All observations were made at an abandoned, concrete cattle trough with two large concrete tanks (3 × 8 m), an entering stream, and a wet area draining the troughs. The depth of the troughs was sufficient to ensure water throughout the year. While observing doves I remained quietly in a car or blind. Observations were made on individual doves from 06:00 to 20:00 h, although few doves were present after 15:00 or 16:00 h. I observed doves at the waterhole for 42 h. Whenever a flock of doves arrived, I selected the first dove to arrive and began observing it for its first two drinking bouts. I then switched to its nearest neighbor, repeating the process until I had observed one to three doves per flock. Because the flocks were changing rapidly and group size shifted frequently, I waited at least 10 min between recording data on flock members. Flock size was recorded when a flock first appeared and at 1 min intervals thereafter.

Data recorded on each dove included: date, time of day, species, group size, and lengths (in sec) for the first and second drinking bout. Drinking bout was defined as the time from when the dove first began drinking until it ceased drinking and raised its head to look around. Doves are capable of swallowing while drinking, and drinking bouts varied from one to 13 seconds.

I tested the null hypothesis that there are no differences in drinking bout length (and thus vigilance) as a function of species or flock size. I used Kruskal-Wallis χ^2 tests to distinguish species differences in the variables, and General Linear Models Procedure (SAS 1985) to determine the contribution of the independent variables to differences in length of drinking bouts (after log-transforming the data).

Results.—The waterhole was frequented by many raptors. For example I saw a Roadside Hawk (*Buteo magnirostris*) kill a Common Ground-Dove, and a Gray Hawk (*B. nitidus*) and a Collared Forest-Falcon (*Micrastur semitorquatus*) make passes at doves at the waterhole. The mammalian predators were a tayra (*Eira varma*) and coati (*Nasica nasua*).

I observed 293 White-tipped Doves and 93 Common Ground-Doves drinking at the waterhole. The best model (SAS Institute 1982) explained 49% of the variation in the length of initial drinking bouts ($F = 118$, df = 3,372) by group size ($F = 319$, $P < 0.0001$), species ($F = 24.2$, $P < 0.0001$), and time of day ($F = 11.2$, $P < 0.0009$). The number of the flock I observed did not enter the model, thus the behaviors of individuals observed within a flock were independent of each other. The smaller ground-doves drank when in smaller groups, but had longer uninterrupted initial drinking bouts than the White-tipped Doves (Table 1). The second drinking bout was significantly shorter in ground-doves compared to White-tipped Doves (Table 1).

TABLE 1
GROUP SIZE AND LENGTH OF DRINKING BOUTS IN DOVES IN COSTA RICA

	White-tipped Dove	Common Ground Dove	χ^2 (*P*)
Number of doves	293	93	
Mean time of day (h)[a]	0952 ± 12.6	1108 ± 12.4	39.1 (0.0001)
Group size[a]	5.9 ± 0.2	7.9 ± 0.4	22.6 (0.0001)
Time for initial drinking bout[a]	4.2 ± 0.1	5.4 ± 0.3	9.6 (0.001)
Time for second drinking bout[a]	4.2 ± 0.5	2.5 ± 0.5	8.7 (0.001)
Correlation of group size and initial drinking bout[b]	0.46 (0.001)	0.60 (0.0001)	
Correlation of time of day and initial drinking bout[b]	NS	0.24 (0.002)	

[a] Given are means ± SE.
[b] Given are Kendall tau correlation (level of significance, NS = not significant).

For both species there was a significant, positive correlation between group size and length of the first drinking bout (Table 1). Time of day was positively correlated with length of the initial drinking bout only for Common Ground-Doves. For both species the mean length of the initial drinking bout increased with group size (Table 2).

White-tipped Doves often drank in groups of 4–5 (max = 16), whereas ground-doves drank in groups of four or more (max = 18). No ground-doves came to the waterhole to drink solitarily.

Discussion.—In the dry deciduous forests of Costa Rica water with cover is limited to a few scattered waterholes. Birds and mammals concentrate near them, and come to drink throughout the day. Just as prey species concentrate near water, so also do predators who are drawn to the waterhole not only for the available prey but for water. Since the waterhole is within the forest, there is cover adjacent to and over the waterhole. The vegetation cover not only provides protection for drinking animals, but it provides hiding places for predators. The hawks I observed attacking doves all waited silently and quietly in the trees for several minutes after the arrival of a flock before making a pass at the doves.

Although the waterhole at Palo Verde provides necessary water for the doves, it also represents a clearly demonstrated, dangerous situation. Since the location of a waterhole is known, it provides a more dangerous threat than foraging because the doves cannot shift locations (as they can with feeding sites). Thus vigilance is crucial to their survival.

The doves at Palo Verde usually drank in groups; less than 4% of the doves drank solitarily, and these were all the larger White-tipped Doves. Given the size range of the raptor predators, the smaller Common Ground-Doves could be taken by any of the raptors, whereas the larger White-tipped Doves could easily fall prey only to the Collared Forest-Falcon (Brown and Amadon 1968).

The doves drink with their heads bowed, making them vulnerable while drinking. Drinking bout time increased with group size, suggesting that individual vigilance behavior decreased. Both species showed a dramatic increase in drinking bout length (decrease in vigilance) with group size. The data from Palo Verde indicate that predators are common and prey on the doves, and that the doves respond by being vigilant. Vigilance for individuals decreased with increasing group size.

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TABLE 2

MEAN TIME FOR INITIAL DRINKING BOUTS FOR DOVES IN COSTA RICA

Group size	White-tipped Dove			Common Ground-Dove		
	N (Flocks)	N (Individuals)	Time (Sec)	N (Flocks)	N (Individuals)	Time (Sec)
1	14	14	1.4 ± 0.1	0	0	—
2	15	23	2.1 ± 0.2	4	4	1.3 ± 0.2
3	26	35	2.6 ± 0.2	6	7	2.2 ± 0.2
4	34	43	3.2 ± 0.3	7	10	2.9 ± 0.2
5	41	59	4.2 ± 0.2	12	16	4.3 ± 0.3
6	26	42	4.6 ± 0.2	13	15	5.3 ± 0.4
7	18	24	4.9 ± 0.3	14	16	5.6 ± 0.3
>8	11	33	7.9 ± 0.5	16	26	8.4 ± 0.6

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JOANNA BURGER, *Dept. of Biological Sciences, Rutgers Univ., Piscataway, New Jersey.* *Received 17 June 1991, accepted 15 Oct. 1991.*

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Observations at a Paradise Tanager nest.—The Paradise Tanager (*Tangara chilensis*) inhabits the canopy and forest edge of tropical forests in the Amazon Basin and Guianan region of South America (Isler and Isler 1987, Ridgely and Taylor 1989). At the Tambopata Nature Reserve in southeast Peru (12°50′S, 69°17′W) it is common in canopy mixed species flocks (Donahue et al. 1987). We observed a nest there from an observation platform in the canopy of an emergent tree.

The nest, in an early stage of construction, was discovered by Donahue on 23 June 1989. It was supported in the fork of a small, leafy branch 31 m above the ground in the outer top edge of an emergent *Ceiba pentandra*. The nest was then observed from a canopy platform in the same tree for a total of 48 h from 23 June to 23 July 1989. The first material observed for nest construction was long, stringy bright green staghorn lichen-like moss. As construction progressed, white, irregular strings of the common Amazonian fungus *Rhizomorpha corynephora* were added to the nest, with the green moss still being predominant. Additionally, the birds used a fluff similar to dandelion seeds and possibly spider web in smaller quantities. Near the end of the construction period straw-like grass was used to line the nest. Construction was last observed on 1 July.

During construction, the birds' visits to the nest site usually lasted one to two min. The frequency of the visits varied (e.g., 24 June ten trips spaced three to fifteen minutes apart over a 2.5-h period, 27 June three trips over 4 h, and 1 July two trips over 2 h during a 5-h observation period). Both members of the tanager pair were present during nest construction. However, only one bird carried building materials on each visit to the tree. Copulation, with the female holding nesting material in her beak, was observed once after the pair had entered the tree. Afterwards, the female placed the moss in the nest. The male moved off into another part of the tree until she had finished. They then left together, silently.

Incubation was first observed 4 July. Incubation sessions varied from 15 to 55 min. As during construction, the frequency of nest visits varied (e.g., 9 July 2 trips over the 3-h observation period, 12 July 6 trips over 4 h, and 17 July 3 trips over 3 h of observation). The incubating bird often left the nest unnoticed, quietly dropping out of the tree. Calling started up only some distance from the nest tree.

The *Ceiba* tree was losing its leaves while the nest was under construction. By 20 July, the tree was leafless and the nest completely exposed. On this date, we first watched the adult pair feed the nestlings. Both members of the pair brought spiders, orthopterans, and caterpillars to the nest. Feeding was observed on 20–21 July only. We watched the pair make two trips over one hour on the first day in the late afternoon and five trips over 3.5 h of observation on the second day. Usually one bird sat on the nest for 40–60 min after both of the birds had delivered their food, one after the other, to the nestlings. Once both birds left immediately after making their deliveries but returned 15 min later with more food. One bird then sat on the nest. On 23 July, the nest was found hanging 5–6 m below the original nest position and out of reach of recovery. The cup-shaped side hung towards our platform. The tanagers were not present. One week later, after a rain storm, there was still no activity and the old nest was gone. It is probable that the nest's complete exposure was responsible for its failure. Indeed, known nest predators, such as toucans, aracaris, and toucanets, had been seen frequently in nearby fruiting trees throughout the observation period.

On 26 August a pair of Paradise Tanagers was seen building a nest in the same tree. Again, the nest was in the outer top edge of the tree crown in a small fork, mostly hidden by leaves. Copulation was observed in a neighboring tree, and again, the female had nesting material

in her beak. The same green moss and the white, stringy fungus were visible as part of the nest. On 3 September the nest was gone, as were the birds.

During nest construction the tanagers frequently were accompanied to the nest tree by Green-and-gold Tanagers (*Tangara schrankii*) and Black-faced Dacnises (*Dacnis lineata*), and less often, by a Turquoise Tanager (*T. mexicana*) and an Opal-crowned Tanager (*T. callophrys*). The visiting birds stayed near the member of the pair not actively nest building. None of the birds foraged during the visit and no aggression was shown by the pair of Paradise Tanagers towards the visitors. The birds made chip notes while in the tree. Later, during the incubation period, a male Green Honeycreeper (*Chlorophanes spiza*) followed the Paradise Tanager into the tree. As the tanager sat on its nest, the honeycreeper moved about in the tree eventually approaching the nest from underneath. The tanager left its nest, sat opposite the honeycreeper until it left, then returned to incubate. During the feeding stage, a female Blue Dacnis (*Dacnis cayana*) was chased out of the tree after it approached and nearly touched the nest from below. The individuals of these six species, along with the pair of Paradise Tanagers, seemed to be permanent members of a large mixed species flock that we frequently observed in the vicinity of the *Ceiba pentandra* tree between January and September 1989. When we watched these species interact with the Paradise Tanagers at their nest, the flock was not seen in the vicinity.

The observations of copulation during which the female held nesting material and the consistent occurrence of only one bird carrying nesting material suggest that the female is at least predominantly responsible for nest building. This contradicts Ruschi's (1979) report of pairs building the nest together. According to Isler and Isler (1987), females of the genus *Tangara* typically build their nests alone, although they are attended closely by the male. Tanager males not actually helping the female in construction often accompany her while she gathers material or may sing or call nearby while she works on the nest (Skutch 1989). This is consistent with our observations, as the bird not actively constructing hopped about in the tree, chipping frequently, after arriving with its mate.

The cup shape of the Paradise Tanager nest, typical of tanagers as a whole (Skutch 1989) and of the *Tangara* genus specifically (Isler and Isler 1987), is consistent with the only description of a *Tangara chilensis* nest (Ruschi 1979). However, the nest elevation of over 30 m is higher by more than 10 m.

It was not possible to determine whether both sexes participated in incubation, as the sexes are alike, and the bird that came to incubate arrived at the tree alone. Most likely, the female was solely responsible for incubation, as is typical for tanagers (Isler and Isler 1987). The observed incubation range of 13–17 days agrees with Ruschi (1979), Isler and Isler (1987), and Skutch (1989).

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TERESA M. WOOD, *P.O. Box 554, Machias, Maine 04654;* FRANK GALLO, *33 Urban St., Apt. 2, New Canaan, Connecticut 06840;* AND PAUL K. DONAHUE, *P.O. Box 554, Machias, Maine 04654.* *Received 6 Feb. 1991, accepted 20 Nov. 1991.*

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Observations of the breeding biology of the Elfin Woods Warbler.—The endemic Elfin Woods Warbler (*Dendroica angelae*) was first described in 1972 from the Caribbean National Forest, Luquillo Mountains, Puerto Rico (18°19′N, 66°45′W) (Kepler and Parkes 1972). Initially thought to be restricted to the Luquillo Mountains (Kepler and Parkes 1972), the species was later reported in other mountain ranges on the island, although it is still considered rare (Willis 1972, Gochfeld et al. 1973, Perez-Rivera and Maldonado 1977). The first Elfin Woods Warbler nest was found in the Luquillo Mountains by Wiley (1985). Between 1977 and 1985, Wiley (1985) located four additional nests in the Luquillo Mountains, but detailed observations on breeding biology are lacking. I found Elfin Woods Warbler nesting in aerial leaf litter in the Maricao State Forest in western Puerto Rico. I here present the first observations of its breeding biology. The species currently is being considered for threatened or endangered status (U.S. Fish and Wildlife Service 1989).

Study area.—The Maricao State Forest is located in the Cordillera Central mountain range in western Puerto Rico (18°09′N, 66°58′W) and covers 4150 ha. Mean annual rainfall is 2346 mm, mean annual temperature is 22°C, and relative humidity fluctuates between 60% and 90% (Colon et al. 1976 in Cruz and Delanoy 1984). Three life zones are recognized within Maricao State Forest boundaries: subtropical moist, subtropical wet, and subtropical lower montane (Ewel and Whitmore 1973). Five plant associations also exist there: Maricao mixed-hardwood, forests derived on volcanic soils, Maricao windy ridge, lower montane palm forest, and *Podocarpus* mixed-hardwood.

Methods and materials.—The following variables were measured at active nest sites: percent ground cover (ocular tube), percent canopy cover (ocular tube), shrub density (counting number of shrubs along two perpendicular transects within the sampling plot that were intercepted by my outstretched arms), diameter at breast height (dbh) of trees (diameter tape), canopy height (clinometer), nest height (clinometer), and altitude (altimeter and topographic map) (James and Shugart 1970, Cruz and Delanoy 1984). All measurements were made within a 0.01-ha circular plot centered on the nest. Nest components were identified, whenever possible, as to plant species. Nest measurements included inner diameter, outer diameter, height, and depth, all measured with a dial caliper (±0.1 mm). I used 7 × 35 binoculars to observe the warblers. No blind was used, but the warblers appeared to behave normally. Time spent by adult Elfin Woods Warblers at the nest was recorded to the nearest second using a stopwatch, and the number of visits to the nest was counted. The standard observation period was 08:00–11:00, with observations varying from one to five days between 4 April and 8 May 1990. Each observation period was subdivided into hourly intervals to assess behavior differences during the morning. Arthropods brought to the nest were identified as to order, whenever possible.

Results.—I discovered a nest under construction on 30 March 1990 at an elevation of 750 m within the *Podocarpus* mixed-hardwood association, of the subtropical lower montane Life Zone. A second nest was found in the same area on 27 April 1990.

Trees within the 0.01-ha circular plot of the first nest included *Cecropia peltata* (1),

Byrsonima wadsworthii (1), *Podocarpus coriacea* (3), *Linociera dominguensis* (1), *Magnolia borinquensis* (1), and the tree fern *Cyathea aquilina* (4), all of which ranged from 7.6 cm to 15.2 cm in diameter at breast height. The sample plot had 70% ground cover, 80% canopy cover, shrub density of 450 stems/ha, and a mean canopy height of 10.6 m.

The nest was placed at 7.6 m above ground within dry aerial (suspended) leaf litter, which consists of dead leaves that have fallen from canopy trees and have become entangled or caught among vegetation and/or vines (Munn and Terborgh 1979, Gradwhol and Greenberg 1982, Rosenberg 1990). The first nest was placed within three *Cecropia* leaves suspended on an upright fork of the inner portions of a 7.8-m tall *B. wadsworthii* tree.

The second nest also was within a dry *Cecropia* leaf, but was only 1.3 m above ground. This nest was found destroyed by predators on 29 April 1990. No observations of nest building, parental behavior, or microhabitat were recorded at the second nest.

The first nest was a tightly woven, open cup made of black rootlets and fibers from tree fern stems or both, dry leaves of *Chusquea abietifolia* and *B. wadsworthii,* and dry strands of *Panicum maximum* leaves. The rootlets are flexible when moist, but become like small wire springs when dry, thereby serving as an inner framework that preserves the shape of the nest basket (Collias and Collias 1984). The interior of the cup was lined with fibers of *C. abietifolia,* dry grass leaves (probably strands from *Arthrostylidium sarmentosum*), and some vegetal down. The second warbler nest contained all of the above materials as well as some down feathers. The first nest measured 45.3 mm inner diameter, 79.5 mm outer diameter, 51.9 mm high, and 38 mm deep and has been deposited in the Western Foundation for Vertebrate Zoology, Los Angeles, California.

The first nest was built by both parents. The female usually arrived at the nest first, producing a "chip" contact note (very similar to that of wintering Black-throated Blue Warblers [*Dendroica caerulescens*]). The female did not leave the nest until the male made a similar contact note. The male then entered the nest while the female remained on a nearby perch. After another exchange of notes, the male emerged from the nest site and both flew from the nest. This pair of Elfin Woods Warblers approached their nest furtively by at least seven different routes. I observed them together while bringing nest materials to the nest from 30 March to 6 April 1990. From 9 to 25 April, the only activities I observed near the nest were singing by the male and only the male entering the nest. The pair were not observed together, and the female was not seen. From 27 April to 9 May, both parents brought food items to the nest, and begging calls from at least two individuals could be heard. No activity was observed after 9 May. The nest was collected on 17 May. On 11 June, I observed adult Elfin Woods Warblers feeding an immature 200 m away from the nest-site described here, but I do not know if this was the pair from the first nest.

Average time (±SD) spent by parents at the nest during period 1 (N = 33 visits, $\bar{x}$ = 33.9 ± 69.4 sec, range 3–320 sec) was longer than mean time spent at nest during period 2 (N = 53 visits, $\bar{x}$ = 16.2 ± 23.3 sec, range 1–105 sec) and period 3 (N = 62 visits, $\bar{x}$ = 11.9 ± 17.6 sec, range 1–80 sec). Time spent by parents at the nest decreased after 09:00.

Both the male and female brought food items to the nest. On 20 (16.1%) of 124 trips, food items were identified: nine lepidopteran adults, nine orthopteran adults, and two lepidoptera larvae.

Discussion.—Both Elfin Woods Warbler nests were associated with aerial leaf litter. There are at least two possible reasons for such a concealed nest-site. One is reduced exposure to predation. Possible avian predators that may have exerted selective pressure for nest-site selection of the Elfin Woods Warbler include the now extirpated White-necked Crow (*Corvus leucognaphalus*) (known to have preyed upon passerine nestlings), Sharp-shinned Hawk (*Accipiter striatus*), and Pearly-eyed Thrasher (*Margaropus fuscatus*), which are common nest predators at Maricao (Wetmore 1927, Biaggi 1983, Delanoy and Cruz 1988). Several

genera of carnivorous mammals (known only from fossil remains) and two endemic snakes also may have exerted selective pressure for nest-site selection of the Elfin Woods Warbler (Biaggi 1983). At Maricao State Forest, roof rats (*Rattus rattus*) and small indian mongooses (*Herpestes auropunctatus*) (recently introduced exotics) are presently major predators of bird eggs and chicks. Nest-site choice and behavior exhibited by the Elfin Woods Warblers before entering and leaving the nest suggest predation as a likely selective factor for nest-site selection of this species.

Other functions of domed or covered nests are shedding rain and/or providing shade (Collias and Collias 1984). Skutch (1967), Collias and Collias (1984), and Stiles and Skutch (1989) noted that some wood warblers in Costa Rica, as well as other small passerines in the tropics, conceal their nests by placement (e.g., ground leaf litter, vegetation) as well as by structure (roofed nests). The Elfin Woods Warbler follows the tendency of 15 West Indian wood warblers (Bond 1985) of selecting nest-sites at low to moderate heights (1.3–7.6 m) above ground, but placement of nests among aerial leaf litter is unique among wood warblers. In this case, the three dry *Cecropia* leaves (successful nest) and one *Cecropia* leaf (unsuccessful nest) provided the equivalent of a roof for the Elfin Woods Warbler nests. However, the dead *Cecropia* leaves disintegrated during nest collection, suggesting that while *Cecropia* leaves provide effective concealment, nest sites are fragile. Therefore, the apparent strategy for this species is to be as furtive as possible in entering and leaving the nest, because if the nest is discovered by a predator, it can easily be destroyed because of the structural fragility of the *Cecropia* leaves.

The nest location made it impossible to gather data on clutch size, and number of hatchlings or fledglings, but presence of at least two hatchlings could be inferred (by asynchronous begging calls). Apparently, nesting of Elfin Woods Warblers occurs between April and May, because all five Elfin Woods Warbler nests found by Wiley (pers. comm.) were at egg stage in April, while immatures were observed by Kepler and Parkes (1972) during the summer months (May–July) of 1971.

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Bryan Arroyo-Vazquez, *Dept. Biological Sciences, Univ. of Arkansas, Fayetteville, Arkansas 72701* (Present address: *U.S. Fish and Wildlife Service, 611 East 6th Street, Room 449, Austin, Texas 78701*). *Received 30 April 1991, accepted 12 Nov. 1991.*

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Vulnerability and mortality of young Australian Magpies on roads.—The process of development from hatching to the adult varies in the time required for each stage, the amount of learning required to master the necessary skills, and the type of learning or skill required. Nevertheless, the young of all birds must learn to cope with a variety of hazards once they leave the relative safety of the nest. Often the early aspects of learning that take place before or after fledging are ignored, although Bateson (Proc. 19th Int. Ornithol. Congr. 1116–1126, 1988) and others have extensively studied imprinting. The period following departure from the nest is particularly traumatic because young birds must learn to forage by themselves, to recognize appropriate foraging and roosting habitats, and to avoid predators and other dangers. One problem for many species in the modern world is to avoid vehicles on roads, particularly those birds that scavenge on animals hit by cars. This problem is increasing as more roads are built and as dirt roads are paved.

Study area and methods.—This study was conducted along primary and secondary roads in the South Island, New Zealand from 4 November to 8 December 1990. We travelled a

TABLE 1

AUSTRALIAN MAGPIE COUNTS ALONG 1803 KM OF MAJOR PAVED ROADS ON SOUTH ISLAND, NEW ZEALAND

	Dead on road	Live on road	Within 25 m of road	26–50 m from road	51–75 m from road
One young	53	44	44	21	3
One adult	0	23	41	42	45
One adult and one young	0	9	22	27	18
Two adults and one young	0	1	1	3	4
One adult and two young	0	2	6	11	21
One adult and three young	0	0	2	5	3
Total sightings		79	116	89	94
Total young		58	79	88	76
Total adults		36	73	91	95

variety of roads east of the mountains from Kaikoura to Dunedin, recording Australian Magpies (*Gymnorhina tibicen*) as a function of age and their location relative to the road. Data were recorded in 5 km stretches, and we did not include towns or cities in our censuses. We noted the presence of all magpies, the size and age composition of groups, and their location in five categories: dead on road, alive on road, within 25 m of the road, between 28–50 m of the road, and 51–75 m from the road. We did not record birds more than 75 m from the road. We also noted the presence of other dead animals on the road for comparison.

To examine the magpie's avoidance of roads with fast-moving traffic, we conducted a separate series of censuses on paved highways and on adjoining dirt roads that were perpendicular to the highways. Thus the habitat was similar. Each census was of 5 km of a dirt road, and the adjoining 5 km of paved highway. These data are not included in our overall census data.

Results.—We observed 603 live magpies and 53 dead magpies along 1803 km of roads. All dead magpies were young. In the same distance we also saw the following dead animals: Four Marsh Harriers (*Circus approximans*), eight South Island Pied Oystercatchers (*Haematopus ostralegus*), three Mallards (*Anas platyrhynchos*), 273 Brush-tailed possum (*Trichosurus vulpecula*), 99 European rabbits (*Oryctolagus cuniculus*), eight hedgehogs (*Erinaceus europaeus*), and five ferrets (*Mustela furo*). For all the other species of birds, both adult and young were found dead on the road. Although both young and adult magpies were found in all locations relative to the road, more young than adults were closer to the road (Table 1). Over 85% of the solitary young were within 18 m of the road, whereas only 53% of the solitary adults were there ($\chi^2 = 34.9$, df = 1, $P < 0.001$). Further, parents with young were even less likely to be within 18 m of the road (32%, N = 43) than within 18–54 m (68%, N = 92). Thus, although solitary adults feed within 18 m of the road, they generally keep farther away when they have young ($\chi^2 = 5.2$, df = 1, $P < 0.05$).

For 10 censuses (each 5 km), there were significantly more magpies along side roads than along paved highways (Table 2, $\chi^2 = 121.8$, df = 1, $P < 0.001$).

Discussion.—We found that all of the dead magpies found on the roads were young. There are two possible reasons for this finding: (1) young have more difficulty finding natural foods

TABLE 2
COMPARISON OF AUSTRALIAN MAGPIE COUNTS ON MAJOR PAVED HIGHWAYS WITH COUNTS ON DIRT ROADS RUNNING PERPENDICULAR TO THEM

	Dirt roads	Major paved roads
One young	22	6
One adult	32	9
One adult and one young	26	10
One adult and two young	13	3
One adult and three young	7	
Two adults and one young	12	1
Two adults and two young	1	
Two young	5	
Two adults	2	
Total	120	29
Total young	119	23
Total adults	108	24

and so rely on dead carcasses on the road more often than do adults, and (2) they are less able to perceive and avoid an oncoming vehicle. In almost all studies where age differences have been examined (see Burger, Proc. 19th Int. Ornithol. Congr. 1127–1140, 1988), young have more difficulty finding or capturing food. Thus it is not surprising that young magpies might be so handicapped. We found significantly more young magpies feeding on the road than adults, suggesting that they use the available food on the road more than do the adults. Only young were killed by vehicles. Whenever we could, we noted the distance between our oncoming car and the magpies when they flushed. Whenever both were present, adults always flushed before young. Thus it seems likely that young magpies are killed on the highways both because they forage there more often and because they wait longer to flush from oncoming vehicles.

Not surprisingly more magpies were near (within 54 m) secondary roads than near paved highways. As the habitats were similar, this difference shows either avoidance of paved roads or that unwary magpies near highways were already killed, reducing the "paved road" population.

Dhindsa et al. (Environ. Conserv. 15:303–310, 1988) suggested that in India granivorous birds are attracted to roads, and that insectivorous and other birds are repelled by them. They attributed this to the grain spilled on roads in India. However, in New Zealand, magpies on the highways and secondary roads were primarily eating road-killed animals and were often killed while flying from this food source.

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JOANNA BURGER, *Dept. of Biological Sciences, Rutgers Univ., Piscataway, New Jersey 08855;* AND MICHAEL GOCHFELD, *Environmental and Community Medicine, UMDNJ-Robert Wood Johnson Medical School, Piscataway, New Jersey 08854.* *Received 9 Sept. 1991, accepted 18 Nov. 1991.*

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Great Shrike-Tyrant predation on a Green-backed Firecrown.—On 26 July 1990 (11:45 EST) at Reserva Natural Las Chinchillas (north-central Chile, 31°30'S, 71°06'W) I observed a Great Shrike-Tyrant (*Agriornis livida*) capture a Green-backed Firecrown (*Sephanoides sephanoides,* Trochilidae) at a mistletoe patch (*Tristerix aphylus*). After dropping to the ground, the Great Shrike-Tyrant slammed the hummingbird against the ground with sideways jerking motions. It then flew away with the hummingbird's limp body in its bill. Great Shrike-Tyrants are robust birds (about 100 g, Humphrey et al. 1970) with large, powerful, hooked bills. They are solitary and secretive but fairly common in the Mediterranean semiarid thorn-scrub vegetation of north-central Chile (Philippi 1964). Darwin states that he "was assured by the inhabitants that it is a very fierce bird and that it will attack and kill the young of other birds" (in Crashway 1907, p. 70). At Las Chinchillas, Great Shrike-Tyrants prey on lizards and large insects (J. E. Jiménez, unpubl. data). My observation indicates that they are also capable of preying on hummingbirds. Stiles (1978) has suggested that Tiny Hawks (*Accipiter superciliosus*) catch hummingbirds by waiting quietly ("still-hunting") near territorial perches and flower clumps. My observation suggests that "still-hunting" near flower clumps may also be used by Great Shrike-Tyrants to catch hummingbirds.

The rarity of predation observations on North American hummingbirds has prompted Miller and Gass (1985) to conclude that predation is not a significant risk for hummingbirds in temperate habitats and that biologists are justified in ignoring predation as a factor influencing hummingbird feeding behavior (see Lima 1991 for a contrasting view). In tropical habitats, predation by Bat Falcons (*Falco rufigularis,* Beebe 1950) and Tiny Hawks (Stiles 1978) may not justify this assumption. Jiménez and Jaksic (1989) report remains of *S. sephanoides,* the most abundant Chilean hummingbird, in pellets of Austral Pigmy-Owls (*Glaucidium nanum*) at Reserva Natural las Chinchillas. Only further observations will establish if predation by Great Shrike-Tyrants and Austral Pigmy-Owls represents a significant risk to foraging hummingbirds in Chilean semiarid habitats.

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Carlos Martinez del Rio, *Dept. of Ecology and Evolutionary Biology, Princeton Univ., Princeton, New Jersey 08544-1003.* *Received 30 July 1991, accepted 24 Oct. 1991.*

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Observations of an adult hummingbird provisioning an incubating adult.—Among hummingbirds, only females invest heavily in nest construction and nestling care (Wolf and Stiles 1970). Incubation and feeding of nestlings are almost always performed by a single adult female. Males engage in indirect activities such as territory defense and nest guarding, if they contribute to the nesting effort at all (Moore 1947, Wolf and Stiles 1970, Snow 1973). Although circumstantial evidence exists for males incubating eggs (Moore 1947, Schafer 1954) and feeding young (Schafer 1954, Clyde 1972), in few cases have the presumed males been sexed unequivocally, and in no cases have these anomalies proved to be general phenomena. Wagner (1952) reported cases where more than one female Blue-throated Hummingbird (*Lampornis clemenciae*) shared incubation at a single nest. However, direct food provisioning to an incubating individual previously has not been reported for a hummingbird. This note is the first account of an adult Band-tailed Barbthroat (*Threnetes ruckeri*) provisioning a second, incubating adult on the nest.

Our observations were made in a primary lowland rain forest about 35 km SE of Golfito, Province of Puntarenas, Costa Rica. From 18–20 January 1991 we observed a single Band-tailed Barbthroat nest from a distance of 15 m with 10 × 50 binoculars. The nest, containing two eggs, was hanging beneath, and was therefore sheltered by, a large leaf (*Heliconia* sp.) approximately 2 m above the bank of a brooklet. Two *T. ruckeri* in adult plumage attended the nest. Neither bird showed plumage characteristic of a subadult bird (e.g., buffy feather edges would indicate a recently fledged bird; W. Baltosser, pers. comm.). Both individuals were within 3 m of the nest simultaneously for 2.35 h of the 16 h of observation. In all cases when both individuals were present, one was incubating and the other either perched within 1 m of the nest, hovered near the nest, or flew in the general vicinity of the nest. We were unable to recognize individuals based on plumage. However, we believe the two maintained their respective roles, since during each incubation bout the nonincubating individual repeatedly flew from its perch, hovered directly in front of the incubating bird, and returned to its perch. In 73 out of 219 (34%) of these approaches, bill contact occurred between the birds; the hovering bird inserted its bill into the open gape of the incubating bird, flexed its throat muscles, and exerted its tongue, indicating the transfer of food. At least one approach with feeding occurred during each incubation bout. After most approaches (both with and without provisioning), the nonincubating bird returned to its perch and called.

We were unable to sex these birds unequivocally by observation alone. The incubating individual was likely a female. The nonincubating individual may have been a female that had lost her clutch or brood and had begun cooperating with the nesting female. Alternatively, this bird may have been feeding her own brood, and once those young were lost, continued to feed but at another nest where incubation was still in progress. It is also possible that the second adult was a male, in which case we witnessed a very uncommon event. Although we have no evidence to suggest that this provisioning incident is characteristic of *T. ruckeri*

or hermit hummingbirds in general, further intensive studies of the breeding biology of this avian group may yield some interesting surprises.

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Kyle E. Harms and Jorge A. Ahumada, *Dept. of Ecology and Evolutionary Biology, Princeton Univ., Princeton, New Jersey 08544.* *Received 16 May 1991, accepted 11 Oct. 1991.*

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A case of aggregated nest placement and probable polygyny in the Swainson's Warbler.—Field studies of wood warblers (Parulinae) have shown that their mating systems are more complex and variable than previously suspected (cf Verner and Willson 1969, Ford 1983, Morse 1989). In particular, facultative polygyny may be widespread in wood warblers. In the most thoroughly studied species, Prairie Warbler (*Dendroica discolor*), polygynists are usually monoterritorial but occasionally defend widely spaced territories (Nolan 1978). The distance between simultaneously active nests of females mated to the same male ranged from 50 to 300 m ($N = 36$; $\bar{x} = 124 \pm 59$ m). Female wood warblers mated to monoterritorial polygynists defend exclusive territories. Aggregated nest placement, the tight clustering of nests within a territory, is unknown in wood warblers. Here I report an unusual case of aggregated nest placement and the first probable record of polygyny in the Swainson's Warbler (*Limnothlypis swainsonii*). The breeding biology of this uncommon species remains poorly known, owing to the inhospitable nature of the habitat where it reaches its greatest abundance—wooded floodplains of rivers in southeastern North America. The bulk of what

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Fig. 1. Nests of Swainson's Warbler placed 2.8 m apart in St. Martin Parish, Louisiana: (top) nest exhibiting typical construction (see Meanley 1971); (bottom) atypical nest lacking bulky outer layer of dead leaves. Eggs are pure white.

is known is due to the efforts of Meanley (1945, 1966, 1969, 1971). Of the approximately 30 nests found by Meanley over the course of 50 years of field work, none was believed to have been the product of polygynous matings (pers. comm.).

On 2 May 1991 (15:00 h), I found two active Swainson's nests (Fig. 1), 2.8 m apart, near the center of a male's territory on the east bank of the Whiskey Bay Pilot Channel of the Atchafalaya River, St. Martin Parish, Louisiana. The nests were placed in the understory of tall second growth woodland (15–20 m tall) dominated by cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), boxelder (*Acer negundo*), and roughleaf dogwood (*Cornus drummondi*). I noticed the higher (0.95 m above ground) of the two nests from a distance of 8 m, but did not see the lower nest (0.4 m above ground) until the warbler flushed in front of me in the undergrowth as I moved closer. The first bird flushed a split second later, and both warblers performed a rodent-like display on the ground, with wings and tails drooped, accompanied by soft chipping vocalizations. The higher nest contained three and the lower nest four eggs in the early stages of incubation. The lower nest was atypical in lacking a bulky outer shell of dead leaves (Meanley 1971). Both warblers returned to incubate within 20 minutes. The male singing nearby had an unusual song dialect that I tape recorded. Neither incubating warbler was mist netted, but I assume that both were females (plumages of sexes are indistinguishable), since incubation by males is unknown (Meanley 1971).

On 12 May, I returned briefly and found that the higher nest was tipped to the side and abandoned. One egg was missing; the other two, which contained large, well-developed embryos, and the nest were collected (USNM 48023). The unhatched eggs of the lower nest were attended by an incubating bird. The male that had been present on 2 May was again singing.

Although male-female interactions were not observed, the circumstantial evidence for polygyny is substantial. Because the nests were near the center of a vigorously defended territory, it is unlikely that the females were mated to different males. Swainson's territories are exceedingly large (pers. obs.) compared with territory sizes of most species of wood warblers (Nolan 1978, Morse 1989) and male defense of territory is strong for an extended period of time. In southern Louisiana, males arrive and establish territories during the first and second weeks of April, defend them vigorously until early July, and continue to sing, at least sporadically, until the first week of September. Males respond aggressively to playbacks of songs from neighboring, and especially non-neighboring, males (pers. obs.). The territorial boundary of the closest neighboring male was approximately 150 m north of the nest site.

Because the Swainson's breeding biology is so poorly known, I can only speculate on whether this case represents opportunistic or facultative polygyny. Vigorous defense of large territories, the norm for this species, may be correlated with the establishment of monoterritorial polygyny (Slagsvold and Lifjeld 1988). However, other factors associated with polygyny, such as sexual dimorphism or low population density, do not seem responsible in this instance. The population density of Swainson's Warbler in May 1991 along the Whiskey Bay Pilot Channel was among the highest ever recorded (ca 17 singing males/km^2) (see Meanley 1971). Meanley (1971) reported that the dry weights of the second and third nests built in one season are progressively lighter than the first. This suggests that the less bulky lower nest (Fig. 1, bottom) may have been built by a female whose earlier nesting effort failed. Because the male's territory included many suitable nesting sites, it is puzzling as to why a second female would build a nest so close to the first.

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GARY R. GRAVES, *Dept. of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.* *Received 1 Oct. 1991, accepted 1 Dec. 1991.*

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Buff-throated Saltator eats army ants.—The relationship between army ants and birds in Neotropical forests has been studied carefully by Willis and others (see Willis and Oniki 1978, and included references). The birds that attend the ant swarms forage upon the invertebrates and small vertebrates that flee the ants (Willis and Oniki 1978), and several bird species obtain virtually all of their food from this source. Although a number of species of birds occasionally eat adult ants, and some woodpeckers are specialists on ants (Bequaert 1922, Schubart et al. 1965, Short 1982, Willard et al. 1991), the attendant species at army ant swarms do not ordinarily eat the army ants themselves (Willis and Oniki 1978), despite some initial confusion about this issue (see Bequaert 1922). The few army ants recovered from the stomachs of attendant species (Willis and Oniki 1978, Sick 1984, pers. obs.) were probably due to accidental ingestion of ants that were on prey items. The only certain report of a bird intentionally eating army ants is by Lancaster (1966), who noted that an incubating Slaty-breasted Tinamou (*Crypturellus boucardi*) ate some when a swarm passed over the nest. However, there are no published records of attendant species deliberately eating army ants. Here I report the first confirmed exception to this pattern, a record of a Buff-throated Saltator (*Saltator maximus*) feeding on army ants (*Eciton burchelli*) in the Reserva Florestal Rio Doce, about 30 km north of Linhares, Espírito Santo, in eastern Brazil.

I observed a small swarm of army ants along the edge of disturbed forest near a marsh on 8 August 1988 at about 12:25. The swarm had attracted only a few birds: Squirrel Cuckoo (*Piaya cayana*), Planalto Woodcreeper (*Dendrocolaptes platyrostris*), White-shouldered Fire-eye (*Pyriglena leucoptera*) and Cocoa Thrush (*Turdus fumigatus*). After watching the activity for about 5 min, I became aware of repeated bill-snapping coming from a vine tangle about 4 m up in a small tree. Because the insects that army ant attendants eat are fleeing from the

moving columns of ants, actively foraging birds at ant swarms usually move about and do not remain foraging at a single site for long, so I investigated.

I found that a column of *E. burchelli* was moving up the tree trunk, and that a Buff-throated Saltator was picking off ants one by one as the ants ran by. In five min of observation, before the bird flew away, it made over sixty gleans from the trunk. Of those, at least half resulted in the capture of an ant. On at least two occasions, the ant captured was one of the large soldiers, but most ants were workers. The saltator was unquestionably eating the ants, not using them for some other purpose. The other ants in the column showed no apparent response to the removal of a small number of their colleagues.

After the saltator left, I examined the ant column carefully. All the ants were *E. burchelli,* and none was seen carrying anything. It seems extremely unlikely that the saltator was obtaining anything other than adult army ants in its foraging efforts.

The Buff-throated Saltator is rare at army ant swarms. Despite thousands of hours observing birds at ant swarms, Willis (1986) reports only 30 records of this common and widespread species at swarms. On several occasions, he observed saltators pecking at insects on trunks, and on one occasion he believed that it was possible that army ants were the target, when they engaged in behavior similar to that reported here. This raises the possibility that Buff-throated Saltators infrequently, but regularly, eat army ants.

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Douglas F. Stotz, *Committee on Evolutionary Biology, Univ. of Chicago, Chicago, Illinois 60637, and Division of Birds, Field Museum of Natural History, Roosevelt Rd. at Lake Shore Dr., Chicago, Illinois 60605.* (Present address: *Museu de Zoologia, Universidade de São Paulo, Caixa Postal 7172, São Paulo, SP CEP 01064, Brasil.*) *Received 23 May 1991, accepted 6 Dec. 1991.*

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Second record of the Flammulated Owl in Nuevo Leon, Mexico.—On 21 June 1991, I visited the Cerro El Potosi (24°52′N, 100°13′W), some 25 km northwest of Galeana, Nuevo Leon. At an elevation of 3700 m, I collected a male (testes black 1 × 1 mm) specimen of Flammulated Owl (*Otus flammeolus*). The specimen (UANL 1933) is deposited in the collections of the Univ. Autonoma de Nuevo Leon. This is the second record from Nuevo Leon, and the third in northeastern Mexico. The A.O.U. check-list (Check-list of North American birds, 6th ed., American Ornithologists' Union, Washington, D.C., 1983) reports this species from La Esperanza in Nuevo Leon (without date). Three places bear this name, probably the locality it refers to is Cerro La Esperanza (25°16′N, 100°09′W, elevation 2000 m) in Santiago. The present record is the southernmost and highest for the species. The distribution and abundance of this owl is not well documented in Mexico because of its apparent rarity (Friedmann, Griscom and Moore, Distributional check-list of the birds of Mexico. Part I. Pacific coast avifauna. Cooper Ornithological Club, 29:138, 1950). Also, the tail (70 mm), and the middle toe without claw (14 mm) are longer than the description. This population probably is isolated and may represent a new subspecies. Additional specimens and fieldwork in appropriate habitat in Nuevo Leon are needed and may confirm this position.

Armando Jesus Contreras-Balderas, *Laboratorio de Herpetologia y Ornitologia, F.C.B., U.A.N.L., Apartado Postal 425, San Nicolas de los Garza, N.L., Mexico 66450.* *Received 3 Sept. 1991, accepted 6 Dec. 1991.*

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ORNITHOLOGICAL LITERATURE

AVIAN GENETICS: A POPULATION AND ECOLOGICAL APPROACH. By F. Cooke and P. A. Buckley (eds.). Academic Press, London, England, 1987: xvi + 488 pp., 58 text figs., 50 tables. $102 (hardcover), $39.95 (paperback).—The great expansion of research into the ecological and population genetics of birds that has occurred in the last 20 years has demanded the publication of a summary volume. Fred Cooke and Paul Buckley are to be congratulated in responding to this demand by producing a very well-edited and attractive book, for an intended audience of ecologists, population biologists, and ornithologists wanting to learn genetic techniques applicable to natural avian populations.

The book is organized into three parts. Part I describes techniques for assaying variation in Mendelian genes, quantitative polygenic systems, chromosomes, allozymes, and DNA sequences. Part II provides detailed summaries of the population genetic topics of philopatry and inbreeding, gene flow, genetic structure, natural selection, non-random mating, and geographic variation and speciation. Finally, in Part III, a selection of long-term studies is presented to illustrate how genetics is integral to understanding population-level phenomena in natural populations.

In Chapter 1, Buckley makes the point that most data on Mendelian inheritance of phenotypic characteristics in birds involve plumage patterns and plumage polymorphisms. For other than a handful of species, however, we do not have sufficient inheritance data to test hypotheses of genetic control of these phenotypes. He also draws the attention of field workers to the existence of threshold polygenes, primarily because segregation ratios can mimic those of simple Mendelian characteristics. For example, he noted that the essentially continuous range of plumage variation in the Variable Oystercatcher (*Haematopus unicolor*), which I had earlier ascribed to a major gene with epistatic modifiers (Baker, Notornis 20: 330–345, 1973), could equally well be accounted for by threshold polygenes.

Boag and van Noordwijk give a fine exposition of the theory and application of quantitative genetics in Chapter 2. They are to be lauded for their extremely balanced treatment of the advantages and problems associated with the analysis of polygenic characteristics. Quite rightfully, they stress that techniques such as heritability analysis artificially partition phenotypic variation into its causal components. Increasing attention is now being directed to "norms of reaction" to understand how a particular genotype can give rise to a range of phenotypes. I am uneasy over the genetic determinism implicit in current quantitative genetic models, wherein the genotype is assumed to be translated essentially one-to-one into the phenotype (with some environmental modulation). My unease stems from the assertion by epigeneticists such as Ho and Saunders (J. Theor. Biol. 78:573–591, 1979) that during development, the genotype specifies only a general algorithm that interacts dynamically with the environment to produce variable phenotypes. If the latter model is correct, then one cannot necessarily conclude that phenotypic resemblance between relatives has an additive genetic basis, but rather could be due to similar environmental induction.

In Chapter 3, Shields summarizes our scant knowledge of bird chromosomes, a deficiency that arises because their minute size (particularly of microchromosomes) makes it difficult to see them, let alone investigate their structure and homology. A conjunction of karyological and molecular studies may allow more progress in the future. New mapping strategies using X-rays and in situ hybridization with DNA probes tagged with a fluorescent dye make it possible to locate genes on chromosomes, and this approach could be fruitful for birds.

The detection and analysis of variation in allozymes is summarized in Chapter 4 by Evans. I found this chapter to be somewhat disappointing in that it was almost pedantic with respect

to details of laboratory technique, an overemphasis on problems of gel interpretation, and a bias towards fragmentary evidence for selection operating at allozyme loci. Evans repeats the old chestnut that it is not possible to test for neutrality, but that it is invoked only when evidence for selection has not been found (which he suggests may result from not looking at relevant parameters). The reverse is true; until the neutral theory of molecular evolution was formulated, it was not possible to generate specific quantitative predictions about the amount and organization of genetic variation in populations (Kimura 1983, Cambridge Univ. Press, Cambridge). Furthermore, Evans ignores the most comprehensive analysis of the nature of genetic variation in birds carried out by Barrowclough et al. (Current Ornithol. 2:135–154, 1984), wherein it is concluded that allozyme data fit predictions of mutation-drift neutral theory.

The first section concludes with an excellent chapter by Quinn and White on the analysis of DNA sequence variation. Because molecular approaches are providing incredible insights into the evolutionary past without reference to phenotypes, it has been suggested that population genetics is no longer a cohesive discipline (see Clark, Mol. Biol. Evol. 5:90–96, 1988). My own view is that researchers working at the phenotypic level will increasingly collaborate with molecular biologists or that they will acquire training in molecular techniques. The synthesis of phenotypic, allozymic, and DNA sequence variation within and among populations is required before we can truly appreciate the evolutionary forces acting on lineages. For example, subspecies of Canada Geese (*Branta canadensis*) are only weakly structured in their nuclear genes because of male-mediated dispersal between breeding ranges. However, mtDNA is structured into two clonal assemblages that presumably diverged in different glacial refugia. Breeding-site philopatry of females and maternal inheritance of mtDNA has preserved this subdivision in mitochondrial genes until the present day (Shields and Wilson 1987, Van Wagner and Baker, J. Mol. Evol. 31:373–382, 1990).

Although biologists are well aware of the viability consequences of close inbreeding, the consequences of philopatry are open to debate. In Chapter 6, Greenwood summarizes current thinking on inbreeding, dispersal, and optimal outbreeding. I know of no convincing electrophoretic evidence in support of high levels of inbreeding in birds, although Greenwood thinks this could be misleading because of wide confidence limits to estimates or that they may be confounded by selection or low levels of dispersal. The last two objections can be ruled out, however, because gene flow among contiguous demes is high, and evidence for selection at allozyme loci is almost totally lacking in birds.

Those interested in direct and indirect methods for estimating gene flow and the genetic structure of populations will be delighted with the insightful review by Rockwell and Barrowclough in Chapter 7. They conclude that *equilibrium* populations of birds thus far studied are only very weakly structured, consistent with high estimates of gene flow. It cannot be overemphasized that many continental populations of birds, especially those in regions that were formerly glaciated during the last ice age, are unlikely as yet to have reached an equilibrium between gene flow and mutational input. Indirect methods (Slatkin, Science 236:787–792, 1987) using private alleles or by inverting Wright's formula $F_{ST} = 1/(1 + 4Nm)$ to obtain the gene flow estimator (Nm) are invalid under non-equilibrium conditions.

Part II concludes with a chapter by Price and Boag on the detection and measurement of natural selection on phenotypic characters in natural populations of birds. They use the Lande and Arnold (Evolution 37:1210–1226, 1983) approach to measure selection on correlated characters, which requires knowledge of heritabilities and genetic correlations between characters. While they are strong advocates of this approach, Price and Boag also point out problems associated with the stability and estimation of genetic correlations and selection of characters, as well as the need for very large sample sizes. They give an example of selection operating on Medium Ground-Finches (*Geospiza fortis*) during the 1977 drought

on Isla Daphine Major in the Galapagos, which yields the counterintuitive result that beak width has been selected to decrease, whereas body size and beak depth have been selected to increase. Yet in the original population of 640 birds prior to the selection event, these three characters were all positively correlated (Table 3). This presumably must mean that the 97 survivors were large-bodied and possessed deep but relatively narrow bills, and this further implies that in large birds there is a non-linearity in the covariance of bill depth and width. A scatter plot (Fig. 5) of residuals from the regression of beak width on six independent variables is used to argue against non-linearity, but the beak depth observations cannot be identified within the cloud of data points. This is a crucial point, because the calculation of selection differentials is based on linear regression of the phenotypic characters. Measurement error is a potentially confounding factor here, especially since beak width is difficult to measure with good precision (although Grant and his colleagues report high repeatabilities for *G. fortis* measured in different years—see Grant et al., Biol. J. Linn. Soc. 23:1–39, 1985).

Non-random mating and its effects on the structure of populations is the subject of Chapter 9. Findlay explains that population patterns of non-random mating cannot be interpreted as evidence of true mating preferences, because the latter is exercised by individuals who may vary in their choice, especially given different availability of mates and ecological constraints. In Chapter 10, Corbin investigates the relationship between geographic variation and speciation. He concludes that there is evidence of a major reorganization of genomes either during or following speciation for the genera he has analyzed. This conclusion is suspect, however, because it is based on differences in slope of plots of F_{ST} against Nei's *D* within and among species. This relationship is inescapably curvilinear if the within and among species comparisons are treated as one array, as previously noted by Barrowclough (J. Field Ornith. 55:509, 1984). In the Epilogue, Buckley defends Corbin's conclusion of bilinearity, but it seems likely that the reduced slope for the within-species regression is induced by gene flow among populations rather than indicating that genetic revolutions accompany speciation. Evidence is accumulating from electrophoretic studies that, although founder effects can accelerate population divergence in birds, both intraspecific and interspecific diversity can be explained by gradual divergence in isolated populations of small to moderate size (Baker et al., Evolution 44:564–582, 1990).

The case histories presented in Part III are all impressive examples of the role of genetic analyses in understanding the population biology of birds. Van Noordwijk's assessment of the quantitative ecological genetics of Great Tits (*Parus major*) is a stimulating insight into not only what is known about this much-studied species, but also what needs to be done to clarify the interactions of genetics with environmental conditions. The observation that heritability of nestling body size is high in years when food is abundant but is zero in seasons when food is scarce clearly indicates that environmental influences can swamp genetic "control" of body size. Such environmental modulation of phenotypes *within* populations should warn researchers of the potential dangers of rigid selectionist interpretations of phenotypic variation, as did James' (Science 221:184–186, 1983) discovery of an unexpectedly large environmental component of phenotypic variation *within* populations.

Parkin summarizes his studies of the evolutionary genetics of House Sparrows (*Passer domesticus*) in Chapter 12. This work is impressive for its scope and thoroughness. Using Ohta and Kimura's (Genet. Res. 22:201–204, 1973) formula for neutral alleles, he calculates that present day populations in Britain should have heterozygosities of 61–74%. Since predicted levels are much higher than he actually observed with protein electrophoresis, he concludes that bottlenecks may have reduced levels of heterozygosity. However, this discrepancy can be accounted for in other ways. First, the long-term effective population size is almost certainly much smaller than current census population sizes. Second, the majority of electrophoretically detectable alleles may be slightly deleterious, in which case hetero-

zygosity will increase only slowly with population size (Kimura 1983). Although Nei's *D* can in theory be used to estimate divergence times of different populations, these estimates are only rough approximations, given the vagaries of sampling errors (particularly across loci). Parkin's assumption that present day populations are in equilibrium is also questionable, given the short time frame since the last glacial period.

The final case histories by Cooke on the Snow Geese (*Chen caerulescens*) and O'Donald on the Great Skua (*Catharacta skua*) are highlights of the book. They demonstrate how major long-term studies of bird populations can accumulate the sample sizes and detail necessary to test sophisticated genetic hypotheses. As such, they should be required reading for all aspiring and practicing population biologists.

I very much enjoyed reading the Epilogue, where Buckley draws together an excellent synthesis of past and future research. With such a wide ranging review, it is almost inevitable that some errors should creep in. For example, it is manifestly *not* true that birds have lower levels of heterozygosity than other vertebrates; birds and mammals have very similar degrees of within-population genetic variation (Avise and Aquadro, Evol. Biol. 15:151–185, 1982). The overall impression gained from this volume is that we currently have relatively little evidence in support of natural selection maintaining polymorphism in bird populations. Researchers should, therefore, heed Buckley's plea "that as a working null hypothesis, henceforth all avian plumage polymorphisms should be considered selectively neutral, and that tests be designed solely to falsify that null hypothesis. If such falsification were demonstrated, then and only then, on a case-by-case basis, would it be reasonable to attempt falsification of carefully crafted alternative hypotheses." Furthermore, this kind of rigor is now possible at the level of morphological evolution among populations. Although natural selection is doubtless involved in the adaptive moulding of phenotypes, its role has usually been assumed *a priori*. Simple null models of phenotypic evolution (e.g., Hill and Lynch, Evolution 40:915–935, 1986; Lynch, Evolution 42:455–466, 1988; Turelli et al., Evolution 42:1085–1089, 1988) allow testing of alternative mechanisms such as genetic drift and mutation. Rejection of neutral models should be a prerequisite for investigating the action of selection on quantitative characters.

I strongly recommend this fine volume to all ornithologists despite its hefty price.—Allan J. Baker.

Birds of the Lower Colorado River Valley. By Kenneth V. Rosenberg, Robert D. Ohmart, William C. Hunter, and Bertin W. Anderson. Univ. of Arizona Press, Tucson, Arizona, 1991: 416 + xv pp., 34 figs., 6 tables. $40.00.—Few regions on earth have been altered by man as profoundly and swiftly as has the lower Colorado River Valley. The damming of the river and the replacement of most native vegetation by the introduced saltcedar (*Tamarix chinensis*) constitute an ecological upheaval affecting all of the American Southwest. This book describes how this upheaval is reflected among birds. Its primary basis is the original research conducted from 1972 to 1986 by a group of biologists under Ohmart and funded largely by the U.S. Bureau of Reclamation. For the historical perspective the authors relied on previously published literature, especially Joseph Grinnell's account of his 1910 expedition.

The genius of this book, and of the research behind it, is its integration of fundamental description, experiment, and theory. Four hundred species accounts constitute the core of the book; these discuss abundance, migration schedules, changes in status, subspecies, habitat, and breeding and feeding habits in a flexible format. Thus basic natural history data provide a firm foundation for further analysis. Among the six chapters preceding the species accounts, one discusses the authors' experiments in reforestation, and another treats more

theoretical ecological problems, as tested by the authors' observations. Although the results of these experiments have been published elsewhere, their being summarized here gives the book a dimension seldom found in regional avifaunas. The recommendations for habitat restoration are grounded in experiment. Reasons for past failures of restoration attempts that wasted government money are explained, and the recurrent irresponsibility of government agencies is illustrated with stories of specific incidents (page 68). I hope that every official with jurisdiction over the Colorado valley reads this book before making another decision.

The authors identify and interpret patterns and trends while also expressing fully the individuality of each species. For example, they describe the direct relationship between structural complexity of a habitat (greatest in cottonwood-willow woodland) and the number of bird species the habitat supports. Yet they also point out that while the distribution of some species may be governed by the structure of the habitat, others are governed by food supply, availability of nesting sites, or temperature tolerance. An important trend the authors note is the decline and loss of migratory, summer-resident insectivores. Yet the apparently irreversible decline of the Willow Flycatcher (*Empidonax traillii*), Bell's Vireo (*Vireo bellii*), and Yellow Warbler (*Dendroica petechia*) contrasts with the recovery of Lucy's Warbler (*Vermivora luciae*), the extension into new habitats of the Yellow-breasted Chat (*Icteria virens*), and the flourishing of the Blue Grosbeak (*Guiraca caerulea*).

A chapter on finding birds in the lower Colorado River valley is helpful but because many roads are not marked or named on the maps in this chapter the visitor will want to equip himself with a detailed road map as well. Other features are a calendar of bird activity (arrivals, departures, peak numbers, singing, nesting, etc.), bar graphs of seasonal status, histograms of numbers of many migrants, and a tabulation of Christmas Bird Count results, the last probably more reliable than those of most such counts elsewhere.

Unfortunately, the authors do not cite the sources for specific records, perhaps because of the "general space limitations" mentioned on page 117. If the Univ. of Arizona Press really imposed such limitations, it has done us a serious disservice. Citations of original sources are fundamental to the verifiability of data that is central to science. The lack of such citations, the only serious defect in an otherwise outstanding book, can only cast suspicion on the data.

The authors did miss a couple of worthwhile opportunities, however. In their history of the ornithological exploration of the Colorado River, they skip from Grinnell's expedition of 1910 to Monson's arrival in 1943. Yet Laurence M. Huey visited the Bard region regularly in the 1920s and 1930s. His collection and field notes are readily available in the San Diego Natural History Museum but are not referred to once in this book. In "Birds of Arizona," Phillips, Marshall, and Monson referred to Huey's collection frequently, so Rosenberg et al. can hardly have been ignorant of it. These data should further illuminate conditions during the last years before the dams changed the Colorado valley forever.

The original data on food habits are based in part on "almost 5,600 bird specimens . . . collected for dietary analysis." These data represent a significant contribution to the book and to the literature on bird diets in general. Yet these 5600 specimens could have been used for other purposes as well but apparently were not. The authors do not mention their disposition. For example, the account of the Brown-headed Cowbird (*Molothrus ater*) implies that 110 individuals were collected over all seasons of the year. These specimens could have provided extensive information on this cowbird's breeding cycle, molt schedule, and dispersal that apparently was not taken or not used. Concerning the cowbird's subspecies, Rosenberg et al. say only "breeding Brown-headed Cowbirds are all presumably *M. a. obscurus*. . . . However, *M. a. artemisiae* Grinnell may occur in winter." By not identifying their 110 cowbirds to subspecies, Rosenberg et al. missed generating information with a

very practical application: if cowbird removal is ever undertaken in the Colorado valley, as it has been in coastal southern California, the trapping should take place at a time and place where the largest numbers of the locally breeding subspecies can be caught. The authors appreciate the applications of taxonomy (for example, see the account of Wilson's Warbler [*Wilsonia pusilla*]), but I'm sorry they missed the opportunity to extend the results beyond those already published by Grinnell, Phillips, and Rea.

The importance and usefulness of this book extend far beyond the visiting birdwatcher or ecologist interested in the adaptations of desert birds. Wildlife managers and park planners anywhere in the Southwest should read the examples showing how native plants can be integrated into a domesticated environment. Residents and tourists need educating on the river's environment and history, lest they think that the deafening hordes of speed-boaters and jet-skiers are the river's indigenous wildlife. Society should know the price it has paid for its thirst for the Colorado.—PHILIP UNITT.

BIRDS OF MALHEUR NATIONAL WILDLIFE REFUGE, OREGON. By Carroll D. Littlefield, illustrations by Susan Lindstedt. Oregon State Univ. Press, Corvallis, Oregon, 1990: 304 pp. $25.95 (hardcover), $15.95 (paperback).—This book is an authoritative reference which should prove to be a valuable addition to the shelf or backpack of any serious birder or traveller who wishes to visit a truly outstanding area for bird observation. If you are a birder, you should not visit Malheur National Wildlife Refuge without first using the book as a guide to help you determine when to go and which portions of this large (73,000+ ha) area to visit. The book is divided into two parts. The introductory portion provides background information of the area. Descriptions of the area are arranged both by geographic areas of the refuge and by the different plant communities within the refuge. Additionally, this section has a chronological guide to the refuge which covers the winter season, the summer season, and both the spring and autumnal migration periods.

Some 240 pages of species accounts comprise the second and major portion of the book. As with most publications of this type, the species accounts and treatments are not perfectly balanced with each other either in depth or detail. Some of the accounts may reveal some of the biases of the author. The unevenness of the accounts occurs primarily with the level of detail offered for particular species, but the uneven treatment detracts from neither the clarity nor usefulness of the book. Each of the species accounts is authoritative, well documented, and provides the types of information needed to further a deep appreciation of the area's importance as either a breeding location or stopover resting spot for the 300+ species that use the refuge.

Carroll Littlefield is certainly well qualified to author this book. He is an accomplished ornithologist and he has spent many years at Malheur National Wildlife Refuge. His knowledge of the habits and populations of the local avifauna is unsurpassed. The literature citation section of the book is acceptable, but not overly exhaustive considering the large number of graduate studies that have been conducted on Malheur National Wildlife Refuge. Refuge files sometimes offer a wealth of chronological and biological data, but are also somewhat inaccessible and certainly ponderous. This is a combination of traits which usually discourages their use. It is obvious that Littlefield spent a great deal of time filtering through the volumes of files at Malheur National Wildlife Refuge and was therefore able to provide the detailed species accounts that this guidebook offers. Now that Littlefield has compiled these records into a more accessible volume, he has increased their value to the ornithological community manyfold.

Carroll D. Littlefield should be commended not only for this contribution to the ornithological community, but for this book as a model for future "Birds of the such-and-so"

volumes. Carroll Littlefield's training as an ornithologist and his thorough knowledge of the Harney Basin are obvious throughout the entire book. It is a valuable contribution to the ornithological literature of the region and provides a thorough guide for a serious birder who is a potential refuge visitor or for the "armchair" birder who wishes to visit vicariously a great birding spot.—Richard B. Stiehl.

An Annotated Checklist of the Birds of Tennessee. By John C. Robinson. Univ. of Tennessee Press, Knoxville, Tennessee, 1990: xi + 276 pp., 33 range maps, 3 numbered text figs., 6 tables. $29.95.—A compilation and synthesis of previously published information must be well organized, arranged in a dependable way, and utilize explicit definitions for categories. John Robinson has done just these things and more in this work. Starting primarily from the rich but cryptically presented notes on the birds of the state that have appeared in *The Migrant,* he has painstakingly reorganized the data into a coherent summary of the distribution and status of 373 species in Tennessee. The work includes thorough coverage through May 1988, as well as noteworthy records from later in 1988. Species accounts include consistent treatment of Status, Abundance, Spring and Fall Arrivals and Departures, Summer and Winter Occurrence, Remarks, and Substantiation. I like the book, which is Tennessee's first book devoted primarily to accounts of species. Robinson suggests the work will be useful to field workers before, during, or after fieldwork. I think its primary use will be as a reference work, for which it is admirably suited. I have had several occasions to use it as a reference, and found it reliable. But the style that makes it useful as a reference makes it dry for general reading. I have few quibbles with the book; one concerns the several range maps arranged as an appendix. The material presented in the maps is interesting, but I am perplexed by the choice of species; many others besides the 33 chosen would be as interesting. The quibbles are minor, however. Robinson's work is a solid foundation from which other work can be launched. The data it contains will be a baseline from which future changes in Tennessee's avifauna can be assessed.—Paul B. Hamel.

Auks at Sea. Spencer G. Sealy (ed.). Cover illus. by John Schmitt. Proceedings of an International Symposium of the Pacific Seabird Group, Pacific Grove, California, 17 December 1987. Studies in Avian Biology No. 14. Cooper Ornithological Society, Los Angeles, California. 1990: 180 + vi pp.—It wasn't so long ago that the pelagic ecology of auks was a mystery wrapped in an enigma. We waved good-by as the irritating birds flew out to sea, and fired off our best guesses a couple of hours later when they came home. We hardly knew where they'd been, let alone what they'd been doing there. The Dovekie (*Alle alle*), perhaps the commonest seabird in the Northern Hemisphere, is still best known as a storm-blown stray. "Auk ecology" was mainly about birds nesting on cliffs or islands—certainly not as members of marine communities. But this bafflement is evaporating with remarkable speed. The pelagic review in Nettleship and Birkhead's "The Atlantic Alcidae" (Academic Press, 1985) has already been overtaken by the papers in this symposium—presented only two years later. I don't doubt that the successor to "Auks at Sea" is already in the pipeline.

The scope is broad but concise. Spencer Sealy's Introduction sets the scene, reminding us of Robert MacArthur's basic zoogeographical principles and the Ashmoles' fundamental contributions to the pelagic ecology of seabirds. The opening section has papers on "Patch Use" and the tactics of foraging: Hunt et al., and Schneider, Harrison et al. in the Bering Sea; Schneider, Pierrotti et al., and Piatt off Newfoundland; Cairns and Schneider, and Gaston and McLaren in the eastern Canadian Arctic. I liked the linking of Least Auklets (*Aethia pusilla*) in the Pribilofs to various indices of zooplankton abundance. I was also

intrigued by the importance of "fronts" there, in concentrating *injured* euphausiids at the surface, to the benefit of Black-legged Kittiwakes (*Rissa tridactyla*) and Red Phalaropes (*Phalaropus fulicarius*) as well as murres (*Uria* spp.). "Allocation of Time and Energy" takes a wider, more strategic view, with the budgets of a piscivore and a planktivore: Common Murres (*U. aalge*) off Newfoundland and Marbled Murrelets (*Brachyramphus marmoratus*) off British Columbia (Burger and Piatt, Cairns et al., Carter and Spencer). Scott, and Duncan and Gaston, describe the swimming migration of young Common Murres and Ancient Murrelets (*Synthliboramphus antiquus*) off the West Coast. There are specialized accounts of diets in relation to available resources: for the Common Murre in Monterey Bay (Croll), Thick-billed Murres (*U. lomvia*) wintering off Newfoundland (Elliot et al.), and various auklets breeding in the Bering Sea (Harrison). The Newfoundland samples were birds taken in the peculiar, legal but unregulated "turr hunt" there. Other auks in peril include the declining Common Murres in central Californian colonies (Takekawa et al.) and the birds killed in the same area by the *Apex Houston* oil spill in 1986 (Page et al.). Finally, Vader et al. summarize the effects on both murres of the decline of capelin (*Mallotus villosus*), an important food in the Barents Sea.

This is a very nice mix of papers presented by leading workers on the pelagic ecology of auks. I particularly liked the comparisons and contrasts at different levels: piscivores vs planktivores, East vs West coasts, Boreal Zone vs Low Arctic. It's a pity we can't yet compare Atlantic Dovekies with the West Coast planktivores or Alaskan auks with Siberian ones. I was disappointed to find only one European contribution; from the pelagic seabird's perspective, the Atlantic is one big Ocean, and should be treated as such. It might be interesting to expand the papers on patch use, and other "energetic" topics by comparisons with baleen whale models. For efficient foraging on euphausiids, a finback (*Balaenoptera physalus*) apparently needs a "patch" at least ten times denser than the overall mean (Brodie et al. 1978. Limnol. Oceanogr. 23:1264–1267). This gives us some kind of bracket for optimum prey densities for auks. However, these niggles are mostly wishful thinking. "Auks at Sea" is an excellent symposium volume, and I recommend it to everyone interested in the pelagic ecology of seabirds.—Richard G. B. Brown.

The Kestrel. By Andrew Village, illus. by Keith Brockie. T. & A. D. Poyser, Ltd., London, England, 1990: 352 pp., 32 black-and-white photographs, 85 numbered text figures, 77 tables, 2 appendices. £18.00.—Ian Newton's significant contributions to our understanding of raptor ecology come from his detailed and precise studies. Andrew Village has clearly learned well from his mentor, and this book compiles a vast amount of data on the Eurasian Kestrel (*Falco tinnunculus*), most of which is derived from Village's own careful studies. The emphasis of this book is on the ecology and regulation of Eurasian Kestrel populations; however, the author leads off with an extremely interesting chapter on kestrels around the world. The term "kestrel" is applied to certain small members of the genus *Falco,* a large genus which also includes the Peregrine (*F. peregrinus*), Gyrfalcon (*F. rusticolus*), Northern Hobby (*F. subbuteo*), and Merlin (*F. columbarius*), to name but a few. Village takes a typological approach towards defining the characteristics that separate "kestrel" species from other members of the genus. He concludes that there is no "clear-cut way of defining" the kestrel group and points out that modern techniques such as DNA-DNA hybridization may help unravel the position of kestrels among the falcons. In lieu of these data, an opinion would have been welcomed. As another student of kestrels, the "group" seems real, though perhaps diffuse, to me.

Several chapters discuss topics that seem to deviate from the theme of population regulation, but are necessary for complete coverage of kestrel natural history. Still, Village

successfully demonstrates the importance that variables such as timing of molt, differential weight gain between males and females prior to egg laying, and seasonal changes in energy budgets have on population dynamics. Two final chapters provide a synthesis of possible mechanisms that regulate kestrel population density. Village concludes that food supply seems to be the primary regulating factor and attempts to characterize the adaptations that kestrels, as well as other raptors, employ to successfully exploit cyclic food resources, such as the voles seemingly so important to kestrels.

Two aspects of Village's research lend themselves to the comprehensive nature of the book. First, Eurasian kestrels were studied year-round, yielding valuable data on winter food supplies and kestrel movements and mortality. This information is essential to discerning and interpreting breeding population dynamics. Second, Village conducted his research in two very different areas of England. In 1976–1979 data were collected in the grasslands of the Southern Uplands of Scotland, while from 1980–1988 most of the data were collected in southeast England in areas of arable farmland. These two areas are extremely different, and by comparing parameters such as food availability, climate, and nest site dispersion between the two sites, Village is able to distinguish different factors that regulate the individual populations. However, since the duration of study in each area is relatively short, some questions, such as population turnover, are, Village admits, difficult to address.

As in any definitive natural history study, this book raises as many questions as it answers. Village does an excellent job of posing questions that his data have failed to address and often usefully speculates on areas where future research would be profitable. As I read the book, I continually jotted ideas down in a notebook for future reference. Village frequently compares his findings with published literature, most frequently that on the European Sparrowhawk (*Accipiter nisus*). There were several places where I felt congeneric comparisons would have been more appropriate, especially considering the voluminous body of literature on the American Kestrel (*Falco sparverius*). Two appendices review the various methods used to estimate kestrel diets and the measurement of home ranges. Though not as comprehensive as the original methodological literature, the appendices are useful for those unfamiliar with the techniques. As a reference for graduate students searching for ideas for a thesis, this book should be required reading.

The format of the book follows closely the style of other Poyser books. Figures are interspersed throughout the text, but tables are arranged at the end. Although flipping back and forth to consult the tables may be distracting, excellent summaries at the end of each chapter facilitate easy understanding. Keith Brockie's illustrations rate as some of the best kestrel drawings I have ever seen and provide a little personality for these birds that Village understands so well.

Although the book skirts more theoretical treatments of population ecology, it provides a broad empirical framework for those treatments to be made by others. The book might bore theoreticians, but for most students of population ecology, birds, and more specifically, raptors, the book is exciting, useful, and inspiring.—Reed Bowman.

Recent Advances in the Study of Neocene Fossil Birds. I. The Birds of the Late Miocene-Early Pliocene Big Sandy Formation, Mohave County, Arizona, by K. Jeffrey Bickart (pp. 1–72). II. Fossil Birds of the San Diego Formation, Late Pliocene, Blancan, San Diego, California, by Robert M. Chandler (pp. 73–161). Ornithological Monographs No. 44. $19.75 ($17.75 to AOU members).—Imagine studying mixed flocks of flamingos, stilts, avocets, plovers, sandpipers, cranes, and huge storks along the edge of a shallow lake in western Arizona, with six species of geese scattered from the grassy shore out to deeper water. Or how about a short pelagic trip off San Diego that features five grebes, three

albatrosses, three shearwaters, two boobies, two gannets, four cormorants, and nine alcids among 35 species of seabirds? These seemingly fanciful situations once were genuine, although well before you or your binoculars existed.

Through the study of fossils, K. Jeffrey Bickart and Robert M. Chandler have illuminated important chapters in the history of North American birds. Bickart describes the avifauna (based on 1000 identifiable bones from 38 species in 13 families) from the lacustrine Big Sandy Formation, near Wickieup, Mohave County, Arizona. This formation is late Miocene to early Pliocene in age, 6.1 to 4.6 million years old. Most species from this interval of time can be referred to modern genera (not necessarily living in North America today), although not to extant species. As expected from lacustrine sediments, the birds are dominated by freshwater species (80% of the bones are from anatids), although hawks, eagles, accipitrine vultures, a dove, and a crow are represented as well. Bickart does an excellent job of describing and interpreting the osteology of anatids, particularly the geese (Anserinae), a most difficult group to classify on the generic or species level. Bickart usually deals effectively with the perplexing situation of trying to decide if his fossils, which include nearly complete associated skeletons, can be reconciled with named species that are based only on a fragment or two. Even though his material is of much greater quantity and quality than that of previous researchers, Bickart is conservative in naming new species. Sometimes, as in the case of the stork *Ciconia* sp. (90 bones from 14 skeletal elements), a more rigorous effort at species-level classification would seem to be warranted.

Bickart reviews the systematic literature for each taxon from the Big Sandy Formation, often exposing unresolved matters. I found this to be helpful, although the account of the supposed shelduck *Anabernicula* was perplexing. After pointing out numerous osteological and systematic problems with this strictly fossil genus, Bickart tentatively referred a nearly complete associated skeleton to *Anabernicula,* prefaced by (p. 35), ". . . it [*Anabernicula*] might include some species that properly belong with the Anserinae, and others with the Tadornini of the Anatinae.

I tentatively refer the Wickieup goose to this genus, although if the genus did not exist, I would unquestionably refer the material to *Branta* in the Anserinae, even though it is so much smaller than any extant goose."

Perhaps the strongest point of Bickart's study is his taphonomic analysis of the Wickieup birds (pp. 54–61). Bickart postulates that massive die-offs, perhaps from botulism, may be responsible for the accumulations of bird bones at Wickieup. He suggests why there are biases in the relative abundances of species and skeletal elements. It is a pity that Bickart overlooked very pertinent research by Jehl (1988, Auk 105:97–101) on death assemblages of modern birds at Mono Lake, California.

Chandler describes the avifauna (2000 identifiable bones, representing about 39 species in 13 families) from the San Diego Formation (late Pliocene marine sediments, 3.0 to 1.8 million years old) of southwestern San Diego County, California. After reviewing previous research, Chandler compiles the entire avifauna for the first time, describing new species and revising classifications as needed. Most of this research seems to be careful and straightforward. One glaring error concerns extinct grebes, where the same specimen (LACM 2113/1071, tibiotarsus) is referred to *Podiceps subparvus* Miller and Bowman on pp. 93–94, and then to *Aechmophorus elasson* Murray on p. 95. An annoyance is the repeated misuse of the obsolete term "Recent" rather than "Holocene" when referring to the geochronological unit that represents the last 10,000 years. This is complicated further by Chandler's frequent misuse of "Recent" as an adjective that really means "modern" or "living." In some cases, the context does not determine which of the incorrect meanings is intended.

Being bound together in a single volume, one cannot avoid comparing the two papers. Neither has an "Abstract," although each has a short "Summary" at the end which reads

just like an abstract. Bickart's paper has fewer errors, an exception being the incomplete sentence about doves on p. 52. Bickart's photographs are better than Chandler's (sharper focus, cut out more carefully, have scale within the plate). Unlike Bickart, Chandler goes to great length to determine character polarities. Bickart presents a more thorough overall picture of his paleofauna, providing good perspective on how the birds from Wickieup compare to others of similar age. Bickart also describes the sedimentary environment and the associated fossil fauna, dominated at Wickieup by large mammals. Neither Bickart nor Chandler mentions the presence or absence of juvenile bones, an indicator of local nesting. In fact, neither author suggests seasonality of their paleofaunas, which is particularly surprising for Bickart, given his interest in taphonomy. Chandler never states whether he regards the marine birds of the San Diego Formation as a nesting colony, a nearshore wintering or migratory avifauna, or a pelagic accumulation of unknown seasonality. In fact, the only community-level interpretation of the San Diego Formation avifauna is in an upbeat, invigorating Foreword to the entire volume by Storrs L. Olson, who points out that the history of North American marine and freshwater avifaunas would be pure conjecture without fossils.

This volume will be of interest to those studying the evolution or ecology of North American waterfowl or seabirds. Like the recent *Ornithological Monograph* No. 45 by Storrs Olson and Helen James on late Quaternary birds from Hawaii, the papers by Bickart and Chandler represent a renewed exposure of paleontology in mainstream ornithological publications. While admirable, the research by Bickart and Chandler would have benefited greatly had they been among the primary collectors of the fossils they studied. The time is ripe for new field work at both the Big Sandy and San Diego formations, using modern techniques of measured stratigraphic collecting, as well as fine-mesh screens to sample the smallest species.—David W. Steadman.

ANNOUNCEMENTS

Southern African Ornithological Society Thematic Symposium

A symposium on the topic "Migration, Dispersal and Nomadism" will be held at Langebaan, South Africa, 12–16 September 1993. The symposium will take place on the shores of Langebaan Lagoon, one of southern Africa's prime wader (shorebird) sites, in the new West Coast National Park. At the time of the conference, the migrant waders will be arriving from their northern breeding grounds, and the spring flowers in the park will, weather permitting, be close to their best. All persons interested in attending this symposium should inform Mr. T. B. Oatley, Avian Demography Unit, Dept. of Statistical Sciences, Univ. of Cape Town, Rondebosch, 7700 South Africa, in order to be put on the mailing list to receive a copy of the First Announcement which will contain further details of the programme. The First Announcement will be posted in late 1992. Anyone wishing to present a paper or a poster should also inform Mr. Oatley. Papers on all aspects of migration will be welcomed, but special attention will be devoted to the Palearctic-African, intra-African, and Southern Ocean migration systems and to the conservation of migrant birds. The concepts dispersal and nomadism will be interpreted liberally, and will include, for example, topics such as the foraging movements of seabirds. Papers presented at the symposium will be considered for publication in a special number of *Ostrich,* the journal of the Southern African Ornithological Society.

North American Bluebird Society Research Grants—1993

The North American Bluebird Society announces the tenth annual grants in aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus *Sialia.* Presently three grants of single or multiple awards are awarded and include:

Bluebird Research Grant.—Available to student, professional or individual researcher for a research project focused on any of the three species of bluebird in the genus *Sialia.*

General Research Grant.—Available to student, professional or individual researcher for a research project focused on any North American cavity nesting species.

Student Research Grant.—Available to full-time college or university students for a research project focused on any North American cavity nesting species.

Further guidelines and application materials are available upon request from: Kevin L. Berner, Research Committee Chairman, College of Agriculture and Technology, State University of New York, Cobleskill, New York 12043. Completed applications must be received by December 1, 1992; funding decisions will be announced by January 15, 1993.

The 1992 research and award recipients are:

Bluebird Grant

Wayne Davis.—A Better Bluebird Box

Student Grants

John P. McCarty.—The Impact of Environmental Variability on the Reproductive Success of the Tree Swallow

Janice Simpkin.—Reestablishment of a Bluebird Metapopulation in Central Nevada and Dispersal Dynamics Within the Metapopulation

Neil Niemuth.—Tracking of Microtine Rodent Populations by Breeding Saw-whet Owls

General Grants

E. Dale Kennedy and *Douglas W. White.*—Effects of Nest Box Size and Microclimate on Breeding Success of Bewick's Wrens

Brad Semel.—The Ecology of Brood Parasitism in the Wood Duck

Charlotte C. Cockran.—Reproductive Success of Western and Mountain Bluebirds in Grasshopper Control Areas, and Potential For Using Bluebirds to Control Grasshopper Densities

Rick Baetsen.—Breeding Biology and Habitat Requirements of the Northern Saw-whet Owl in Northern Michigan, By Surveying Methods and an Artificial Nestbox Program

International Shrike Symposium

Shrike researchers will meet at Archbold Biological Station, Lake Placid, Florida, 11–15 January 1993. Investigators of shrike biology are invited to contribute to scientific sessions. Ornithologists interested in more information should contact Reuven Yosef, Archbold Biological Station, P.O. Box 2057, Lake Placid, Florida 33852-2057.

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The Wilson Bulletin

Editor Charles R. Blem
Department of Biology
Virginia Commonwealth University
816 Park Avenue
Richmond, Virginia 23284-2012

Editorial Board Kathy G. Beal
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P.O. Box 6045
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616 Xenia Avenue
Yellow Springs, OH 45387

Suggestions to Authors

See Wilson Bulletin, 103:163–164, 1991 for more detailed "Information for Authors."

Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Sixth Edition, 1983) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Abstracts of major papers should be brief but quotable. In both Major Papers and Short Communications, where fewer than 5 papers are cited, the citations may be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (AIBS, 1983). Photographs for illustrations should have good contrast and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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Membership inquiries should be sent to Dr. John Smallwood, Dept. of Wildlife and Range Sciences, Univ. Florida, Gainesville, Florida 32611.

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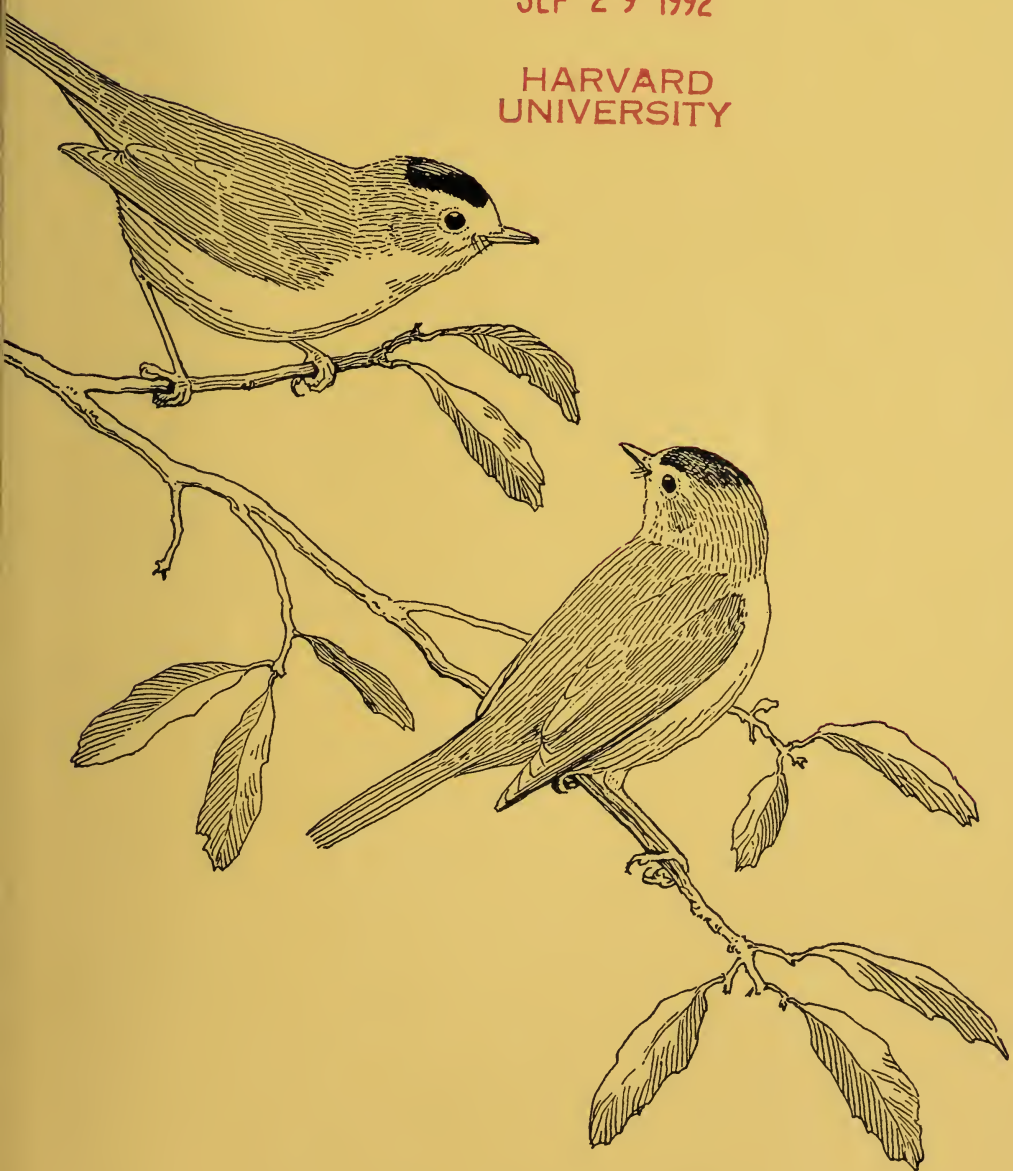

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Cundinamarca Antpitta (*Grallaria kaestneri* sp. nov.), a new species of antpitta from Colombia.

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A NEW SPECIES OF ANTPITTA (FORMICARIIDAE: *GRALLARIA*) FROM THE EASTERN ANDES OF COLOMBIA

F. GARY STILES[1]

ABSTRACT.—The Cundinamarca Antpitta (*Grallaria kaestneri* sp. nov.) is described from a locality at upper subtropical elevations of the eastern slope of the Eastern Andes of Colombia. It is a terrestrial bird of the understory of primary and secondary cloud forest, known from elevations of ca 1800–2300 m at the type locality; its vocalizations, foraging behavior, and probable breeding season are described. The closest relative of the new form appears to be the Santa Marta Antpitta (*G. bangsi*) of the Santa Marta mountains; in fact, *G. kaestneri* may be the present-day representative of the ancestral population that gave rise to *G. bangsi*. The probable distribution, and possible conservation measures for *G. kaestneri* are discussed. *Received 10 Dec. 1991, accepted 13 May 1992.*

ABSTRACTO.—Se describe *Grallaria kaestneri* sp. nov. de una localidad de la zona subtropical alta de la vertiente oriental de la Cordillera Oriental de los Andes de Colombia. Es un ave terrestre del sotobosque de selva nublada primaria y secundaria; en la localidad típica ha sido registrado entre ca 1800 y 2300 m de elevación. Se presentan datos sobre la época de cría, las vocalizaciones, y el comportamiento de forrajeo de la nueva especie, cuya pariente mas cercano parece ser *G. bangsi* de la Sierra Nevada de Santa Marta; incluso, *kaestneri* bien podría ser el representante actual de la población ancestral que dio origen a *bangsi*. Se discuten la distribución probable de *G. kaestneri*, y posibles medidas para la conservación de la especie.

The birds of the eastern slope of the Eastern Andes of Colombia remain poorly known, despite the proximity of this area to the city of Bogotá. Aside from sporadic, isolated collecting efforts far to the north in Boyacá (Olivares 1971, 1974), virtually all ornithological work on this slope has been concentrated along the old Bogotá-Villavicencio trail, or the present highway that follows essentially the same route (Chapman 1917, Olivares 1969). This area was also evidently an important source of "Bogotá" trade

[1] Instituto de Ciencias Naturales, Univ. Nacional de Colombia, Apartado 7495, Bogotá D. E., Colombia.

skins (Meyer de Schauensee 1964). However, it is important to note that the upper part of this area, including the old towns of Chipaque, Choachí, Une, Cáqueza, and Fómeque, is protected by high ridges to the NE from the moist winds blowing off the llanos, and has a dry, rain-shadow climate. As far back as 1913, Chapman (1917) was disappointed by the lack of forest in the region, until he had descended the Río Negro valley to ca 1100 m, on the last ridges above Villavicencio. Even at this early date, the land along the valley floor close to the old trail had been deforested, since for a century or more the trail had been the major trade route between Bogotá and the llanos. Thus, while the birds of the floor of the Río Negro valley have been thoroughly collected, the very wet forests on the adjacent high and very steep ridges have been all but unexplored ornithologically.

On 16 October 1989, Peter G. Kaestner, at the time the U.S. Consul in Bogotá, set out to explore a recently opened road from Monterredondo on the highway, to the town of El Calvario in the valley of the Rio Guaitiquía in the department of Meta. From Monterredondo (elevation 1375 m), one of Chapman's old collecting stations, the road winds steeply up the precipitous ridge of the Cuchilla Llano Grande, eventually crossing the ridgetop at 3200 m before dropping down to El Calvario. On this ridge, patches of remnant forest extend down to 1700–1800 m near the road, and above 2000 m the area is largely covered by very wet cloud forest that extends up to the páramo line. Somewhat disturbed along the road, and broken by scattered pastures, the forest cover in the area has apparently changed little in extent since the first aerial photographs were taken of the area in the late 1960s (Instituto Geográfico Agustín Codazzi, Bogotá). In an area of disturbed forest at ca 2250 m, Kaestner heard an unfamiliar antbird song. Upon recording the song and luring the bird into view with playback, he found it to be an antpitta that he was unable to identify to any known species. Suspecting that the bird represented an undescribed form, Kaestner invited me to accompany him to the site on 19–20 May 1990. On this trip we obtained further observations on vocalizations and behavior, and after intensive efforts with playbacks, succeeded in obtaining a specimen, which left no doubt that the bird indeed represented a new species of *Grallaria*.

With Loreta Rosselli and Luis Miguel Renjifo, I returned to the site on 10–13 January 1991. We were able to obtain two more specimens, plus more extensive information on population densities, elevation range, and behavior of the bird, as well as additional recordings. Unfortunately, further field work in the area has been inadvisable due to an outbreak of guerrilla activity, and I feel it best to wait no longer before describing the new form as

Grallaria kaestneri sp. nov.

CUNDINAMARCA ANTPITTA

HOLOTYPE.—Adult female, no. 30730 of the ornithological collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá; collected by F. G. Stiles and P. G. Kaestner (original number FGS 2746) on 20 May 1990 at an elevation of 2075 m, ca 3 km (7.5 km by road) ENE of Monterredondo, Municipio de Guayabetal, Depto. de Cundinamarca, Colombia. The type locality is almost exactly 50 km SE of the center of the city of Bogotá.

PARATYPES.—Two adult females, nos. 30731 and 30732 of the same collection; collected by F. G. Stiles, L. Rosselli, and L. M. Renjifo on 13 January 1991 at the same locality (original numbers FGS 2781, 2782).

DIAGNOSIS.—Most similar to the Santa Marta Antpitta (*Grallaria bangsi* Allen) of the Santa Marta mountains of N Colombia but considerably smaller and darker, the throat dull whitish with dark mottling instead of bright, immaculate buff, and with the olivaceous color below much more extensive, especially across the chest, with only a small immaculate whitish area on the center of the abdomen, and with the pale streaking of the breast and sides much narrower, essentially restricted to the feather shafts and not set off by narrow dusky borders (see Fig. 1). Comparative measurements of the type series of *G. kaestneri* and two specimens of *G. bangsi* are given in Table 1.

ETYMOLOGY.—I take pleasure in naming this species for Peter G. Kaestner, its discoverer, in recognition of his interest in Colombian ornithology and in appreciation of some fine field companionship. The English name refers to the Department in which the type locality is located, and which doubtless includes a significant part, if not the totality, of the range of the new species.

DESCRIPTION OF HOLOTYPE.—(Color names and numbers follow Smithe 1975, 1981). Crown, nape, back, and scapulars uniform dark olive green (near 48), the feathers with narrow sooty-black fringes and a faint but definite pattern of very fine blackish barring (apparent only in the hand). Lower rump and most upper tail-coverts similar in color but lacking the barring, thus appearing brighter olive-green; tips of longest tail-coverts dark brown; upperside of tail blackish-brown (223, raw umber). Greater secondary coverts, primary coverts, and remiges blackish on inner webs, edged broadly with rich brown (near 223B, verona brown) on outer webs, save that the tertials are darker (223A, mars brown). Lores and facial area dull white, tinged with dull yellowish (near 92, pale horn, but paler), the feathers with dusky bases and dull olive tips (43, grayish olive), producing a heavily mottled appearance; auriculars dull olive with fine pale horn shaft-streaks. Throat whitish, tinged with pale horn, and lightly mottled with grayish olive and dusky (near 119, sepia); feathers of upper chest whitish, broadly tipped with grayish olive; breast, sides, and flanks grayish olive with narrow dull whitish streaks along feather shafts, broadest on sides and flanks; center of abdomen dull white, tinged with pale horn; thighs more brownish (near 37, antique brown); vent to crissum dull olive-buff (near 119C, light drab), the longest under tail-coverts tipped dark brown (123, raw umber); underside of tail dark olive brown (28). Wing-linings cinnamon (near 39). Iris dark brown; maxilla black and mandible slate gray, both shading abruptly to white along tomia and at tip; legs and feet plumbeous to light purplish-gray (cf Fig. 1).

Adult female, ovary postbreeding, two ruptured follicles; old, wrinkled brood patch; skull 75% ossified; starting molt (primary 1 breaking sheath, 2 in sheath, rest old; traces of molt on body).

FIG. 1. Specimens of the Cundinamarca Antpitta (*Grallaria kaestneri*) (right) and the Santa Marta Antpitta (*G. bangsi*) (left). Note differences in size, throat pattern, ventral streaking, and extent of white on abdomen.

PLUMAGE VARIATION.—The plumage of no. 30731 is virtually identical to that of the type, while in no. 30732 the basal olive portions of the feathers of the breast and sides are slightly paler than the tips, producing a slightly smudgy appearance. No plumage variation was detectable among birds seen in the field, undoubtedly including individuals of both sexes (see below). Variation in measurements among the type series is slight (Table 1).

TAXONOMIC AFFINITIES.—The classification of the antpittas (subfamily Grallariinae) was most recently revised by Lowery and O'Neill (1969), who provided the first comprehensive diagnoses for all genera of the group (*Pittasoma, Grallaria, Myrmothera, Hylopezus, Grallaricula*), as well as for the subgenera of *Grallaria* (*Grallaria, Thamnocharis, Hypsibemon,* and *Oropezus*). Placement of *kaestneri* in *Grallaria* is supported by its Type 3 (2-notched) sternum, evident in body skeletons prepared from the paratypes, as well as its distinct tarsal scutellation, including the plantar surface, its distinct but slender rictal bristles, and overall size and proportions. Among the subgenera of *Grallaria, kaestneri* is best assigned

FIG. 1. Continued.

to *Hypsibemon* Cabanis on the basis of its tarsal scutellation, 12 rectrices, and ratios of wing, tail, and tarsus lengths (Table 1, cf Lowery and O'Neill 1969). However, it is smaller than any other species of this subgenus, and the streaking is much less broad and conspicuous on the underparts. Moreover, one of the supposed diagnostic characters of *Hypsibemon,* pale shaft-streaks on the dorsum, is quite lacking not only in *G. kaestneri,* but also in all individuals of *G. bangsi* and most of the Chestnut-crowned Antpitta (*G. ruficapilla)* (in a few there are faint suggestions of shaft-streaks) I have seen. On the other hand, the narrow sooty fringes and faint dark barring of the dorsal feathers of *kaestneri* are shared by *bangsi*; the barring is also faintly suggested in *ruficapilla*, as well as in several species of the subgenus *Grallaria* (*alleni, guatemalensis, squamigera*), but not in any of the species of *Oropezus* I have examined (*flavotincta, hypoleuca, rufula, rufocinerea,* or *quitensis*). This, plus the close approach of the measurements of *Grallaria* and *Hypsibemon,* suggests that these subgenera are closely related and should be adjacent to one another in the sequence, not separated by *Thamnocharis* as in Lowery and O'Neill (1969).

TABLE 1

MEASUREMENTS[a] OF THE TYPE SERIES OF *GRALLARIA KAESTNERI*, AND OF TWO SPECIMENS OF *G. BANGSI*

	G. kaestneri[b]				*G. bangsi*[c]	
	ICN 30730 (holotype)	ICN 30731 (paratype)	ICN 30732 (paratype)	$\bar{X}$	IND 0934	IND uncat.
Exposed culmen (mm)	20.0	17.8	19.5	19.1	21.8	22.5
Total culmen (mm)	21.4	22.4	23.1	22.3	25.7	26.2
Commissure width (mm)	11.5	11.3	11.4	11.4	16.6	16.7
Bill depth at nostril (mm)	6.2	6.1	6.2	6.2	8.8	7.9
Wing chord (mm)	80.3	80.5	78.7	79.8	95.6	91.3
Tail length (mm)	41.3	42.6	44.6	42.8	51.3	50.5
Tarsus length (mm)	42.2	44.7	43.0	43.4	50.2	51.2
Mass (g)	49.4	45.8	47.4	47.5	62.0	
Ratio tail/wing	0.51	0.53	0.56	0.53	0.54	0.55
Ratio tarsus/tail	1.02	1.05	0.96	1.01	1.02	0.99
Ratio tarsus/wing	0.53	0.56	0.55	0.55	0.53	0.56

[a] All measurements made according to Baldwin et al. (1931). All birds were females except IND 0934 which was a male.
[b] ICN = Instituto de Ciencias Naturales, Universidad Nacional de Colombia.
[c] IND = UNIFEM, INDERENA. One other *G. bangsi* (IND 0932), a fledgling male, was examined; its measurements are not given as the bird obviously was not full grown.

The species most similar to *G. kaestneri* is undoubtedly *G. bangsi*, which is also probably its closest relative. Interestingly, *G. bangsi* was also one of the few species endemic to the Santa Marta mountains that Todd and Carriker (1922) considered to have no close relative in either the Colombian or Venezuelan Andes. It is possible that *G. kaestneri* is the present-day representative of the ancestral population that gave rise to *G. bangsi*, possibly reaching the Santa Marta range during a cool period of the Pleistocene. The affinities of *G. bangsi* would thus lie with the Andes of Colombia rather than with those of Venezuela, unlike the majority of subtropical-zone endemics of the Santa Marta range (Todd and Carriker 1922).

VOCALIZATIONS.—Two vocalizations have been heard from *G. kaestneri*: a loud 3- or (rarely) 2-note phrase that undoubtedly constitutes the territorial advertising song; and a piercing double note, given most frequently in response to playback of the song but also occasionally in response to other loud noises, that is probably an aggressive call. Two of the females of the type series were decoyed in to close range by playback of the song; both gave the aggressive call but were not observed to sing. On two other occasions a singing bird was attracted to very close range by playing back the song, but neither of these birds could be captured; one of the birds almost certainly gave the aggressive note as well as the song. If the latter birds were males, it is possible that only males sing, but both sexes give the aggressive call.

The song (Fig. 2A) comprises 3 similar sharp, clear whistled notes that sound like *wirt, wiirt weert*!, although occasionally the final note is omitted. The full 3-note song occupies about 1 sec; the interval between the first and second notes is longer (ca 0.5 sec) than that between the second and third (ca 0.35 sec). Each successive note is slightly longer (0.14, 0.16, and 0.18 sec) and higher in pitch (ca 2.5, 2.8, and 2.9–3.0 Khz). For comparison the song of *bangsi* is described as ". . . a frequently heard, loud, flat *bob white*, reminiscent of a bobwhite's whistle but not strongly upslurred" (T. B. Johnson, in Hilty and Brown 1986).

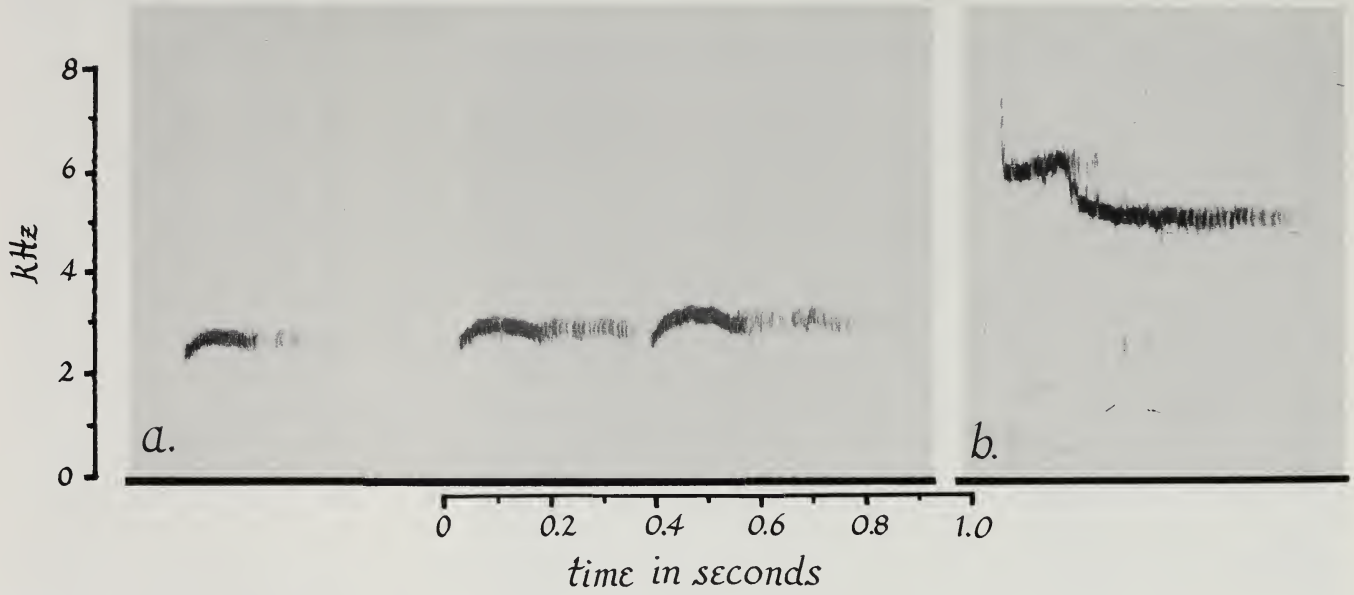

FIG. 2. Vocalizations of the Cundinamarca Antpitta. (a) Territorial song (typical 3-note version; rarely, the last note is omitted). (b) Probable aggressive call.

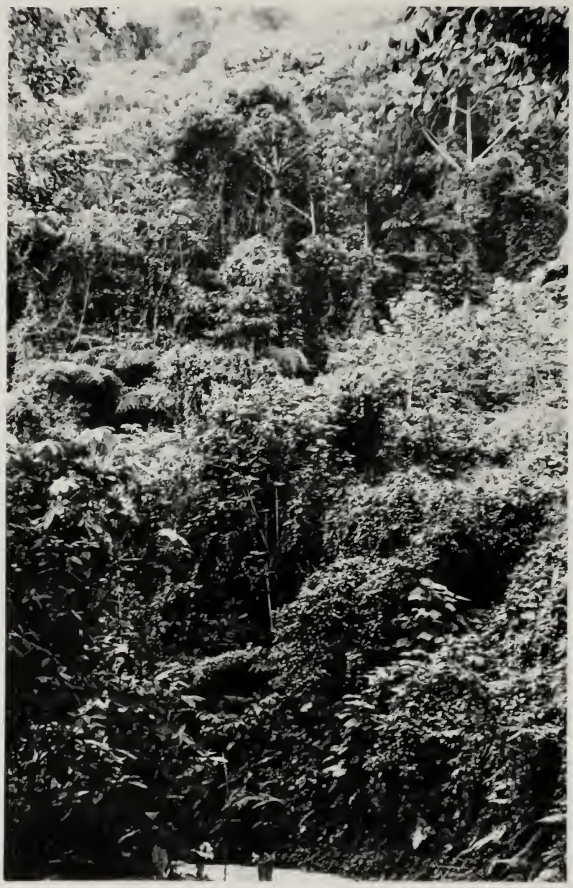

FIG. 3. Habitat of the Cundinamarca Antpitta at the type locality. Note the steep slopes and broken canopy of the forest, with many vines festooning the numerous gaps.

This song thus may not differ greatly from the rare two-note variant of the song of *G. kaestneri.*

The aggressive call (Fig. 2B) is considerably higher in pitch, with a first note at 5.8–6.0 Khz, falling abruptly to a longer note at ca 5.0 Khz. This call sounds like *SEEleee,* the first part in particular being very sharp and piercing.

Similar vocalizations, a loud territorial song and a shorter, sharper note given in response to playback of the song, are given by *G. ruficapilla,* also of the subgenus *Hypsibemon.* The song of this species is the well-known *compra-PAN* or *c'CU-po-PAA* (the first note is very brief and soft, and audible only at close range), but a sharp *pyuu* is given in response to playback of the song, especially at close range (cf also Fjeldsa and Krabbe 1990).

ECOLOGY AND BEHAVIOR.—Along the Monterredondo-El Calvario road, *G. kaestneri* occurs in a relatively narrow elevation band, roughly between 2000 m (where the first continuous forests begin) to about 2300 m. The forests of this zone (Fig. 3) have been lightly

to fairly heavily disturbed, such that in many areas second-growth trees (*Heliocarpus, Cecropia, Trema, Alnus, Casearia,* etc.) predominate over primary forest elements like Lauraceae, Sapotaceae, *Hyeronima, Sapium, Billia,* etc. Due to the steep slopes, frequent natural treefalls, and occasional extraction of timber trees, the canopy is very broken and irregular; larger trees reach 20 m in height, with occasional emergents (probably remnants of the original primary forest) reaching 30 m. In the numerous gaps and openings in the canopy, dense thickets have grown up, dominated by shrubs and small trees (Urticaceae, Compositae, Rubiaceae, *Siparuna* and *Piper*), bamboos (*Chusquea*), large-leaved herbs (Araceae, Marantaceae, Cyclanthaceae, *Heliconia*), and vines, which also festoon many of the trees at the edges of the gaps (Fig. 2). Palms (*Geonoma, Chamaedorea* and *Prestoea*) and tree-ferns are numerous, as are moss and epiphytes (especially orchids, aroids, and bromeliads), indicative of the heavy rainfall and frequent cloud cover in the area. Dense, dark, and virtually impenetrable in older gaps, the understory is fairly open under a closed canopy of taller trees.

G. kaestneri is fairly common in this area, preferring dense, dark understory around the edges of gaps, under a broken to fairly closed canopy. In the ca 5 ha where we have concentrated our observations and collecting, at least four pairs were detected by song on 12–13 Jan 1991 (assuming that a singing bird represents the male of a pair, as explained above). Along 1.5 km of road between this area and the uppermost site at which we heard *kaestneri* singing, at about 2300 m, an additional 10 pairs were detected on these dates. Similar densities were observed by Kaestner in October 1989, and by Kaestner and me in May 1990. To judge from distant songs heard in the early morning hours, the distribution of *kaestneri* extends down to 1800 m or lower on adjacent ridges where disturbance has been less, and forest cover extends considerably lower.

A very terrestrial antpitta, *G. kaestneri* rarely ascends to perches a meter or more above ground, even to sing (unlike *G. ruficapilla,* which frequently sings from perches at eye level or higher). Within its dense habitat, the bird is not particularly shy, and may approach a motionless observer closely. On 12 Jan 1991 I observed a foraging bird at a distance of 2–4 m for nearly a minute. The bird advanced over the ground with long, springy hops, pausing to rummage with the bill in patches of leaf litter, especially in a fallen bromeliad, from which it extracted a 2 cm long blackish beetle that it beat vigorously against a vertical stem before swallowing; it also dug briefly with the bill in a patch of soft ground at the base of a shrub, but without capturing any prey. On 24 June 1990, Kaestner observed a bird turning over leaves in the ground litter, presumably searching for prey. Stomach contents of the three specimens contained mainly insect parts (beetles, roaches, a katydid) with several spider poison claws and the remains of a small earthworm.

None of the three specimens collected was in breeding condition, and two were definitely postbreeding (old brood patches, atretic follicles). The type, taken in May, was starting molt, while of those taken in January one was in worn plumage, the other was completing primary molt. Singing activity in the population was rather low in May 1990, higher in January 1991; according to Kaestner, the birds were singing "much more" in October 1989 than during our visit in May; in two other visits to the area he noted very little singing on 20 January 1990, but high in June. The breeding season of *G. kaestneri* thus falls mainly or entirely in the second half of the year in the study area, which coincides with the middle and end of the rainy season in the Eastern Andes (cf Hilty and Brown 1986).

Also common in the same areas as *G. kaestneri* was its relative, *G. ruficapilla,* a somewhat larger bird that is more partial to scrub habitats (cf Hilty and Brown 1986). One could often hear the two species singing in close proximity, but *G. ruficapilla* was always in the dense low growth in new gaps with no tree cover, while *G. kaestneri* was in the adjacent forest or old second growth, under at least a partial canopy.

The true extent of the geographic range of *G. kaestneri* is unknown, since the bird is as yet known only from the type locality, but it could be fairly continuous along the eastern face of the Eastern Andes, given the lack of ornithological exploration and difficult access to the cool, very wet middle elevations that it evidently prefers. Considerable forest remains at these elevations in many areas along this slope, although below about 1500–2000 m most forest has been cut (J. Hernández-Camacho, pers. comm.). The ability of *G. kaestneri* to occupy fairly heavily disturbed forest and old second growth is encouraging, since this suggests that as long as some tree cover is maintained, the bird may be resistant to local extirpation. A further indication of the lack of ornithological exploration on this slope has been our discovery of several other species along the Monterredondo-El Calvario road, that heretofore were unreported from the Eastern Andes (e.g., *Phaethornis syrmatophorus*). Further field work and possible conservation measures in the area of the Farallones de Medina, some 50 km NE of Monterredondo, where continuous forest extends down to ca 1000 m, seem urgently indicated.

DISCUSSION

It is interesting that of the new species of South American birds discovered and named in recent years, a very high proportion belong to the family Formicariidae, and no less than four are *Grallaria* antpittas: *G. eludens* (Lowery and O'Neill 1969), *G. carrikeri* (Schulenberg and Williams 1982), *G. blakei* (Graves 1987) and *G. kaestneri* (this study). Given that several other species of the genus are extremely poorly known (e.g., *G. milleri* and *G. alleni* in Colombia), the time seems ripe for a more detailed study of the genus, with particular attention to voice. Since these birds are much more often heard than seen in the dense vegetation they inhabit, and respond readily to playback, experiments along the lines of those of Lanyon (1963) may help to define relationships and establish species limits among related forms that show pronounced vocal differences (e.g., *G. hypoleuca* and *flavotincta,* cf Hilty and Brown 1986). Moreover, such experiments may help to evaluate the taxonomic significance of vocal differences, with little morphological differentiation, among populations of certain species (e.g., the Eastern and Central Andean forms of *G. quitensis,* or the Colombian and Peruvian forms of *G. rufula* [cf Fjeldsa and Krabbe 1990, Graves 1987]).

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COLOR PLATE

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ABUNDANCE, FEEDING BEHAVIOR, AND BODY CONDITION OF NEARCTIC WARBLERS WINTERING IN VENEZUELAN MANGROVES

GAETAN LEFEBVRE,[1] BRIGITTE POULIN,[1] AND RAYMOND MCNEIL[1]

ABSTRACT.—We studied the winter ecology of the Northern Waterthrush (*Seiurus noveboracensis*), Prothonotary Warbler (*Protonotaria citrea*), and American Redstart (*Setophaga ruticilla*) in tropical mangroves of northeastern Venezuela. Data were collected by mist netting, direct observation, and forced regurgitation. These allowed evaluation of the seasonal variations in bird abundance, site attachment, body mass, molt activity, and the foraging behavior and diet of each species. The migrant populations consisted of floaters and site-attached individuals throughout the winter, although their abundance showed different seasonal patterns. Most birds used mangroves during only a fraction of the wintering period. Prothonotary Warbler and Northern Waterthrush abundance differed considerably between the spring and fall migration periods, suggesting that different migratory routes are used during both seasons. The temporal and spatial distribution of Prothonotary Warblers and American Redstarts differed according to sex and/or age classes. The mean body mass of Northern Waterthrushes and Prothonotary Warblers varied significantly throughout the winter. Molt activity was limited mainly to body feathers. Foraging in the flooded mangrove habitat was accompanied by modifications of the feeding behavior of each species. *Received 11 Oct. 1991, accepted 20 Jan. 1992.*

Nearctic migrant warblers spend two-thirds of their annual cycle in tropical or subtropical habitats (Keast 1980). For most species, the general distribution and habitat associations on their wintering grounds have been reasonably well documented (Holmes et al. 1989, Terborgh 1989). On the other hand, few studies have quantified the various components of the winter ecology of Nearctic warblers (Rappole et al. 1983, Greenberg 1986, Holmes et al. 1989, Terborgh 1989). This topic is, however, essential in ascertaining the role of these migrant species in Neotropical avian communities (Greenberg 1984) as well as in understanding the demographic variations observed at temperate latitudes (Holmes et al. 1989).

This paper describes feeding behavior and temporal fluctuations in abundance, site attachment, sex ratio, body mass, and molt activity of the Northern Waterthrush (*Seiurus noveboracensis*), the Prothonotary Warbler (*Protonotaria citrea*), and the American Redstart (*Setophaga ruticilla*), three abundant warblers wintering in the coastal mangroves of northeastern Venezuela (McNeil 1982). The warblers' spatial and social behaviors will be discussed in another paper. Our knowledge of the ecology of these species in the winter quarters is still limited to some fragmentary

[1] Dépt. de sciences biologiques, Univ. de Montréal, C.P. 6128, Succ. "A", Montréal H3C 3J7, Canada.

results (Schwartz 1964, Lack and Lack 1972, Diamond et al. 1977, Post 1978, Bennett 1980, Morton 1980, Rappole and Warner 1980, Holmes et al. 1989). Moreover, few studies were conducted in mangroves (Bennett 1980), a habitat highly threatened by tropical deforestation (Terborgh 1989), and one of the most widely used over the wintering period by the warbler species under study (Barruel 1968, Edwards 1972, Lack and Lack 1972, ffrench 1973, Meyer de Schauensee and Phelps 1978, Morton 1980, Hilty and Brown 1986). We attempted to answer the following questions: During which portion of the wintering period is the mangrove habitat exploited? Are the mangroves used consistently by floaters and site-attached individuals? For sexually dimorphic species, is there any difference in the migration pattern according to sex? What physiological constraints (fat accumulation, molt activity) affect the birds in winter? What is the diet of each species on the wintering grounds? Finally, in a flooded habitat such as the mangroves, is the feeding behavior similar to that reported from other tropical habitats?

STUDY AREA AND METHODS

This study was carried out in three coastal mangroves in the state of Sucre, in northeastern Venezuela. The Chacopata site (10°41′N, 63°47′W) was located in a coastal lagoon while the sites of Chiguana (10°29′N, 63°45′W) and Muelle de Cariaco (10°29′N, 63°45′W) were situated on the north and south shores, respectively, of the Gulf of Cariaco. The climate is tropical, with mean monthly temperatures ranging from 19.5° to 32.3°C. Average annual rainfall is 915 mm, with a severe dry season from late November to mid-May. The mangroves were flooded daily by tides except during a three-week period in March when the ground dries out completely. Data were collected from December 1984 through December 1985 in Chacopata and Chiguana, and from September 1986 through August 1987 in Chiguana and Muelle de Cariaco, by mist-netting, direct observation, and forced regurgitation.

Mist-netting sessions were carried out at two-week intervals (each month in Chacopata) on a 4- to 5-ha plot of black mangrove (*Avicennia germinans*). Twelve to fourteen mist nets (3 × 14 m, 32-mm mesh) were set up 50 m apart on two transects in 1984–1985, while 23 mist-nets were erected 25 m apart in 1986–1987. Mist-nets were operated from sunrise to sunset, with a break in early afternoon, for two consecutive days in 1984–1985 and one day in 1986–1987. The trapping effort included 2016, 4704, and 4968 net-h in Chacopata, Chiguana, in 1984–1985 and 1986–1987, and Muelle de Cariaco, respectively.

During mist-netting sessions, all birds were marked with a numbered aluminium band, weighed with a Pesola balance to the nearest 0.25 g (in 1984–1985 only), and examined to determine their age (juvenile or adult), sex, and molt activity. The sex was not determined in Northern Waterthrushes, due to the absence of sexual dimorphism in the plumage coloration (Pyle et al. 1987). Prothonotary Warblers were classified in two categories, adult males and dull plumaged individuals (adult females and individuals in first-year plumage): males were distinguished from females and juveniles by the nape coloration contrasting with that of the back (Pyle et al. 1987). For the American Redstart, all individuals were sexed, and the age of males was also noted (adult or individual in first winter plumage): adult males had a plumage coloration quite different from females, while juvenile males were slightly different from adult females, the orange-yellow colored patches along the breast contrasting

with the yellow underwing coverts (Pyle et al. 1987). The primary molt was evaluated, using the numerical system developed by Ashmole (1962), and that of rectrices by means of the percent of tail feathers in molt. The body-feather molt was determined on a semi-quantitative scale from 0 to 2 (0 = no feather molting. 1 = few, 2 = many) for the wing coverts, back and abdominal regions, leading to a cumulative value ranging from 0 to 6.

A total of 576 h of observation, regularly scheduled, were carried out in the Chiguana site over both years. For each individual observed, we noted the general foraging methods, the foraging heights (0–0.5, 0.5–1, 1–2, 2–3, 3–4, 4–6, 6–8 and 8–10 m), and the foraging sites, divided into four categories: ground, water (water surface, pneumatophores and partially immersed fallen trees), vegetation (foliage and twigs), and air. All observations were made on randomly selected individuals within a period of two minutes to maximize the number of individuals observed.

Each month, birds were forced to regurgitate by administering potassium antimony tartrate (1.5% solution, administered at 0.8 ml per 100 g body mass) following Tomback's (1975) method. This part of the study was carried out 150 m from the Chiguana site to avoid any disruption of migrant populations. Food items (arthropods) regurgitated were counted and identified to order.

We evaluated the biweekly abundance of each warbler species, distinguishing "floaters" (individuals captured only once and never observed thereafter) from "stable" individuals (banded birds observed or recaptured at least once over the same wintering period). The latter were considered present for the entire period between the first and last date of their captures, and their seasonal variations in abundance corresponded to the fluctuations in the number of individuals "present." Only the sites sampled in 1986–1987 were used for that part of the study. The data from 1984–1985 covered two incomplete wintering periods, and it was thus impossible to evaluate accurately fluctuations in the abundance of stable individuals. To determine if bird abundance varied significantly throughout the winter, the biweekly evaluations of total abundance and of the number of floaters and stable individuals were compared to a uniform distribution (G-test for goodness of fit). When floaters and stable individuals showed significant temporal variations, both abundances were compared by a G-test.

RESULTS

Seasonal variations in abundance.—The Northern Waterthrush was the most abundant warbler in the study area, followed by the Prothonotary Warbler and the American Redstart. Each species represented 75%, 20% and 5% of the captures, respectively (Table 1).

Northern Waterthrushes were present in the mangrove sites from early September through early May (Fig. 1), with their abundance varying significantly over that period ($G = 421.3$, df = 16, $P < 0.01$). The number of individuals increased rapidly during September, reached maximum values from mid-October to early February, then gradually decreased until the departure in May. The abundance of stable individuals followed the same general pattern, but they arrived a month later (early October) and were not numerous until early November. Seasonal variations of floaters differed significantly from those of stable individuals ($G = 111.6$, df = 16, $P < 0.01$); floaters were present throughout the winter but slightly more abundant from October to February.

Prothonotary Warblers were captured from early September through

TABLE 1
ABUNDANCE, BODY MASS, AND FORAGING SITE FOR EACH WARBLER SPECIES

	Northern Waterthrush	Prothonotary Warbler	American Redstart
Abundance (number of individuals captured)			
Chacopata	80	12	2
Chiguana (1984–1985)	191	63	13
Chiguana (1986–1987)	121	34	6
Muelle de Cariaco	329	122	39
Body mass			
Number of individuals weighed	391	135	15
Mean body mass (g)	15.86	13.06	8.05
Confidence interval ($P < 0.05$)	0.14	0.17	0.74
Foraging site			
Number (%) of observations for each category			
Vegetation	52 (17)	179 (99)	243 (51)
Ground	117 (38)	1 (1)	0
Water	136 (45)	0	0
Air	0	0	229 (49)
Number of individuals observed	129	32	49

mid-March (Fig. 1), and their abundance varied significantly over that period ($G = 86.6$, df = 12, $P < 0.01$). The number of individuals increased rapidly from early September through October, decreased markedly from November to December, then remained constant until early February, and quickly dropped off thereafter. Both floaters and stable individuals were present during most of the winter but showed different temporal variations in abundance ($G = 26.9$, df = 13, $P < 0.01$). Abundance of stable individuals was high and regular from early October through early February, while floater abundance was much more variable, the disappearance of a high proportion of these individuals being responsible for the drop observed in the middle of the wintering period.

American Redstarts, present from mid-September through mid-April (Fig. 1), were also characterized by significant temporal variations in abundance ($G = 32.9$, df = 13, $P < 0.01$). Their abundance increased gradually until mid-December, then slowly decreased until early April. Floaters were the primary cause of these temporal variations, as the biweekly abundance of stable individuals did not differ significantly from a uniform distribution ($G = 20.3$, df = 13, $P > 0.05$).

Age/sex ratios.—In American Redstarts, females comprised about 85% of all individuals, while two-thirds (6/9) of the males observed were in

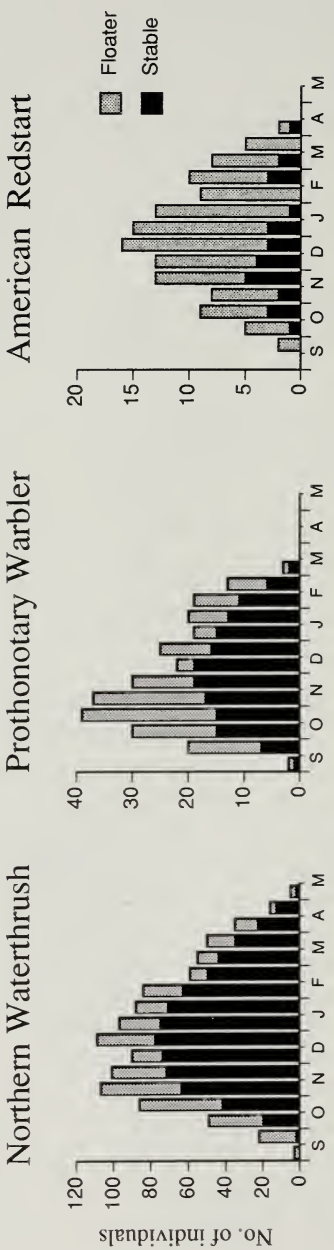

FIG. 1. Seasonal variations in the abundance of floaters and stable individuals of Northern Waterthrushes, Prothonotary Warblers, and American Redstarts in 1986–1987.

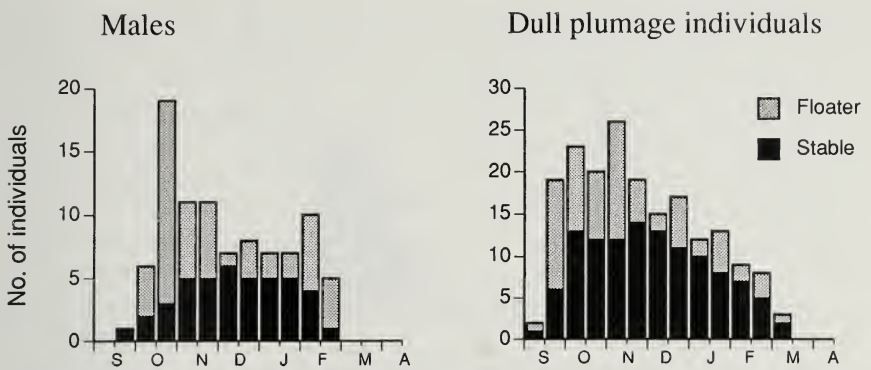

FIG. 2. Seasonal variations in the abundance of floaters and stable individuals among males and dull plumaged individual Prothonotary Warblers (females and juveniles) in 1986–1987.

first-year plumage. In Prothonotary Warblers, 61% of the population was composed of dull plumage individuals, i.e., females and juveniles. The abundance of both types of individuals differed significantly over time ($G = 30.5$, df = 13, $P < 0.01$). Indeed, dull plumage individuals began arriving in early September and were already abundant by mid-September, while adult males arrived in mid-September, with a distinct peak occurring in mid-October (Fig. 2).

Variations in body mass.—We evaluated the mean body mass of each species, using all captured and recaptured birds (Table 1). Temporal variations in body mass were determined only for the Northern Waterthrush and the Prothonotary Warbler (Fig. 3), as few data were available for the

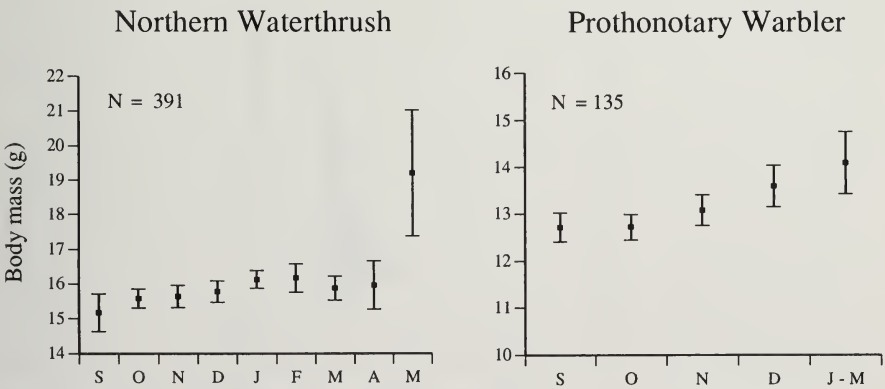

FIG. 3. Mean body mass and confidence interval ($P < 0.05$) of Northern Waterthrushes and Prothonotary Warblers over the wintering period in 1984–1985 (J–M = January through March).

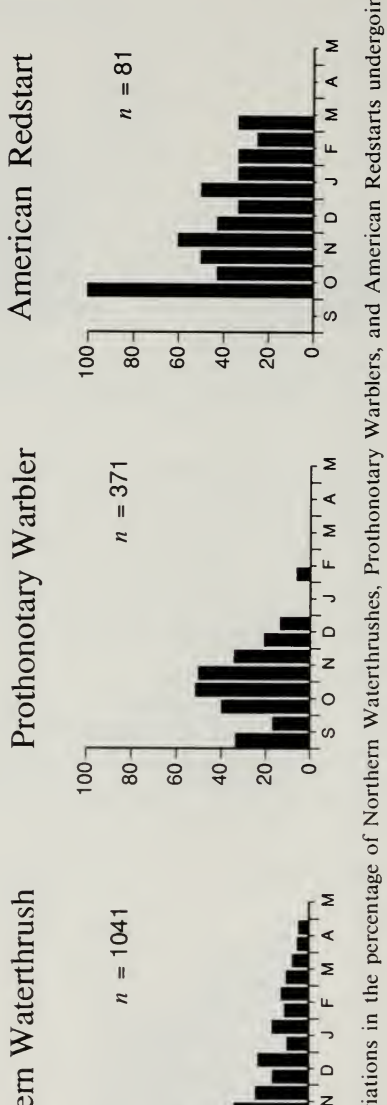

FIG. 4. Seasonal variations in the percentage of Northern Waterthrushes, Prothonotary Warblers, and American Redstarts undergoing body-feather molt.

American Redstart. In Northern Waterthrushes, the mean monthly body mass did not vary significantly from October through April ($F = 2.07$, df = 6,292, $P = 0.056$). Over that period, individuals were significantly heavier than in September ($t = 2.58$, df = 381, $P < 0.05$) and significantly lighter than in May ($t = 6.07$, df = 361, $P < 0.01$). In Prothonotary Warblers, the mean monthly body mass remained constant from September though November ($F = 1.88$, df = 2,100, $P = 0.157$) and from December through March ($t = 1.31$, df = 31, $P = 0.200$, between December and the January–March period), being significantly lower over the first period ($t = 4.65$, df = 134, $P < 0.01$). Although the proportion of floaters was greater during the period of lower body mass in both species, these individuals were not responsible for declining weights. No significant difference was found between the mean body mass of floaters and stable individuals (Northern Waterthrush: $t = 0.470$, df = 296, $P = 0.478$; Prothonotary warbler: $t = 0.712$, df = 115, $P = 0.639$).

Molt.—Primary molt was observed in four warblers only (less than 0.5 % of individuals) and was probably related to the replacement of accidentally lost feathers. Rectrice molt was occasionally observed (in 4% to 7% of individuals). The body-feather molt was, however, regularly noted in many individuals, although each species showed a slightly distinct molt pattern (Fig. 4). In Northern Waterthrushes, the body-feather molt was observed in 19% of individuals and occurred throughout the winter but primarily from mid-October through late December. In Prothonotary Warblers, the body-feather molt occurred mainly from early September to late December and was noted in 29% of individuals. In American Redstarts, the body-feather molt occurred over most of the wintering period and was noted in 38% of the birds. Although body-feather molt was observed over several months in all three species, molt intensity remained low, with nearly 70% of molting individuals having only a few body feathers molting in a single body region.

Diet and feeding behavior.—The three warbler species varied greatly with respect to their diets (Table 2), foraging heights (Fig. 5) and foraging sites (Table 1). The diet of the Northern Waterthrush consisted mainly of Coleoptera, insect larvae, and Hymenoptera (ants), found mostly (85%) from 0 to 1 m above the ground. Some eight insect taxa were occasionally taken, in addition to Araneae, Gasteropoda and Decapoda. The Northern Waterthrush foraged predominantly in aquatic sites, perching on fallen trees (49%) or pneumatophores (51%), and picking up prey either on these substrates or near the water surface. Ground and foliage were less frequently used as foraging sites.

Prothonotary Warblers fed mostly on Coleoptera, Lepidoptera, insect larvae, Hymenoptera (ants), and Araneae, found primarily (60%) from 1

TABLE 2
DIET OF EACH WARBLER SPECIES

Arthropod taxa	Number (%) of food items taken[a]		
	Northern Waterthrush	Prothonotary Warbler	American Redstart
Odonata	2 (0.3)	0	1 (1.8)
Orthoptera	16 (2.1)	1 (1.0)	3 (5.3)
Isoptera	3 (0.4)	0	0
Heteroptera	29 (3.9)	0	2 (3.5)
Homoptera	23 (3.1)	7 (7.1)	17 (29.8)
Neuroptera	2 (0.3)	0	0
Coleoptera	287 (38.2)	42 (42.4)	21 (36.8)
Lepidoptera	5 (0.7)	16 (16.2)	2 (3.5)
Diptera	10 (1.3)	2 (2.0)	5 (8.8)
Hymenoptera	105 (14.0)	10 (10.1)	1 (1.8)
Insect larvae	182 (24.2)	12 (12.1)	3 (5.3)
Araneae	38 (5.1)	9 (9.1)	2 (3.5)
Gasteropoda	35 (4.7)	0	0
Decapoda (*Uca thayeri*)	14 (1.9)	0	0

[a] Number of emetic samples: Northern Waterthrush, 113; Prothonotary Warbler, 39; American Redstart, 15.

to 3 m above the ground. This species foraged in vegetation, using short hops, and captured prey by gleaning almost exclusively on foliage and twig substrates.

The diet of the American Redstart differed from that of the other species by the regular occurrence in its diet of Homoptera and Diptera in addition to Coleoptera. More than 70% of individuals foraged higher than 3 m above the ground. This species fed by gleaning in vegetation as well as by aerial hawking.

DISCUSSION

The Northern Waterthrush inhabits the mangroves throughout the winter, with a higher abundance from October to February. In September, only a few floaters are present. The lower mean body mass observed at this period is similar to that reported in Panama (Rogers and Odum 1966) and in Belize (Mills and Rogers 1990) for postmigrant individuals. From early October, the species abundance rapidly increases, and subsequently the migrant population consists of many site-attached individuals and a few floaters. For most birds, the mangrove study area did not represent the only winter quarters as, in early February (i.e., two months before the onset of the spring migration period in Venezuela, Schwartz 1964), many individuals left the study area without apparent fat accumulation, the mean body mass remaining constant over that period. Neither were the

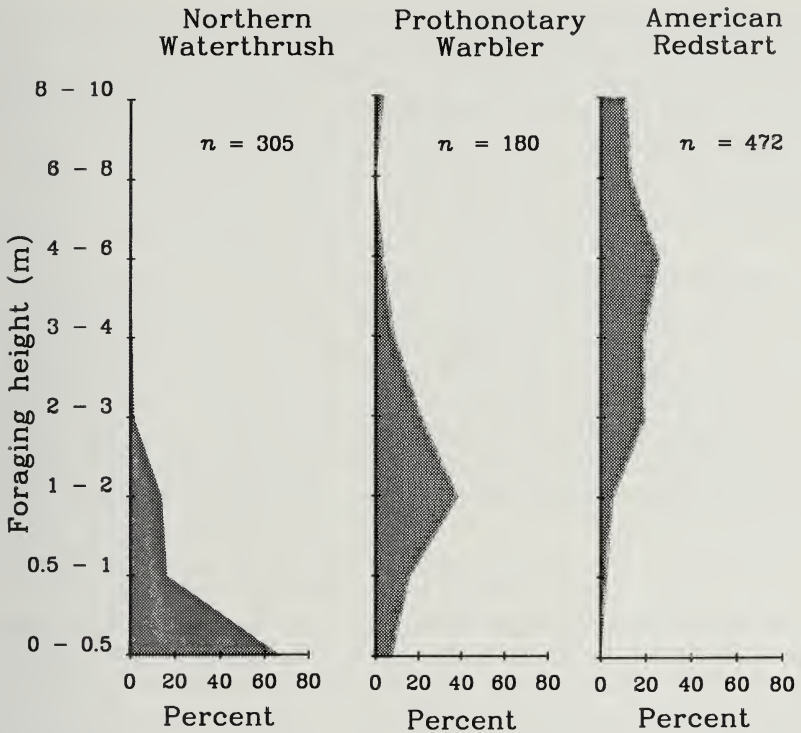

FIG. 5. Percent of Northern Waterthrushes, Prothonotary Warblers and American Redstarts at each foraging height.

mangroves used as transitory migration site in spring, as only a few individuals then were present and undertook the spring migration with a high mean body mass. These results differ greatly from those of Schwartz (1964) for an urban park in Caracas, Venezuela, where most floaters were observed in early winter, and where most site-attached individuals left the area after mid-April. These differences are probably linked to artificial irrigation in those parts of the park where Northern Waterthrushes concentrated from January through the end of the wintering period (Schwartz 1964).

In mangroves, the Northern Waterthrush feeds mostly on Coleoptera, insect larvae, and ants found at the water surface, on the ground, on pneumatophores, on fallen tress, or occasionally in foliage at lower elevations. Thus, a high variety of foraging sites and substrates were used by this species. These results differ from those reported in other tropical habitats (Schwartz 1964, Willis 1966, Post 1978, Rappole and Warner 1980) where the Northern Waterthrush foraged almost exclusively on the

ground. The body-feather molt occurs throughout the winter, but predominantly from October through December.

Some Prothonotary Warblers were present throughout the winter while others used the mangroves during the first half of the wintering period only. Most adult males arrive one month after dull plumage individuals, suggesting some sex and/or age class differences in the fall migration pattern. Many floaters and stable individuals inhabit the mangroves in early winter, a period during which birds undergo body-feather molt and have a significantly lower mean body mass. After the disappearance of a high proportion of floaters in mid-November, the species abundance remains constant until the synchronous departure of all birds in mid-February. These seasonal variations seem contrary to those observed in Colombia (Orejuela et al. 1980, Russell 1980) where the Prothonotary Warbler is present from November through March (Orejuela et al. 1980), with a higher abundance at the end of this period (Russell 1980). Consequently, some individuals wintering in Colombia could have previously passed through Venezuela.

In the mangroves, the Prothonotary Warbler feeds on a great variety of insects, mostly Coleoptera, captured on foliage and twig substrates at low and mid-elevations. The feeding behavior noted in this study (types of prey taken, foraging site and method) are similar to those reported from xeric habitats in Puerto Rico (Post 1978). Only the exploitation intensity of some vertical strata differed: in comparison with Post's (1978) results, the 0 to 1 m stratum was less frequently used in mangroves (24 vs 38%), while the 2 to 3 m stratum was more regularly exploited (21 vs 8%).

For the American Redstart, the coastal mangroves of Venezuela represent a transitory site, primarily used in the middle of the wintering period by a low number of females. The few individuals present in early and late winter suggest that other wintering sites are used then. These could include xeric habitats of western Venezuela, where the American Redstart is present predominantly during the first half of the wintering period (Bosque and Lentino 1987).

In the mangroves, as well as in xeric habitats of Puerto Rico (Faaborg 1984), the proportion of females among the American Redstart population is very high. This suggests a segregation of sexes on the wintering grounds through geographic distribution or habitat association. Nevertheless, the mangrove habitat is not always occupied predominantly by females; mangroves in Jamaica are frequented equally by both sexes (Holmes et al. 1989).

Over the wintering period, the American Redstart undertakes a partial body-feather molt and feeds mostly on Coleoptera, Homoptera, and Dip-

tera captured in the foliage and in the air at high elevations. The foraging height noted in this study differs from those reported by Post (1978) and Bennett (1980) for various Neotropical habitats, including black mangroves. These variations are probably due to the differing foliage height profiles as, in all cases, the American Redstart primarily exploits the subcanopy strata. The foraging methods observed in this study (gleaning and aerial hawking) correspond to those previously reported for this species on the wintering grounds (Post 1978, Bennett 1980).

The Northern Waterthrush, Prothonotary Warbler, and American Redstart differed considerably in their winter ecology. For all three species, the coastal mangroves of Venezuela probably represent a crucial overwintering habitat. Although most birds used the mangroves during only a fraction of the wintering period, they showed some adaptability to mangrove features. Complementary studies of the winter ecology of these warblers on a larger geographic scale and habitat range would be necessary for ascertaining migrant population dynamics and behavioral plasticity of warblers on wintering grounds.

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BREEDING SEASON AND PRODUCTIVITY OF MONK PARAKEETS IN CORDOBA, ARGENTINA

JOAQUÍN L. NAVARRO,[1] MÓNICA B. MARTELLA,[1] AND ENRIQUE H. BUCHER[1]

ABSTRACT.—We studied the breeding productivity of populations of the Monk Parakeet (*Myiopsitta monachus*), at Arroyito and Jesús María, Córdoba province, Argentina. In Arroyito, nests were in introduced eucalyptus trees, whereas in Jesus María nesting was entirely in native tree species. Egg laying started on around 1 November, although onset of breeding varied significantly among years within a three-week period. Start of egg laying within the populations was extended for nine weeks on average. The percentage of occupied nest chambers found with eggs was significantly higher at Arroyito (91%) than at J. María (overall mean 53%). At Arroyito, mean first clutch size was significantly higher (6 eggs) than at J. María (5.4 eggs). Replacement and second clutches were significantly smaller than the first clutches in both areas. Hatching success did not differ between areas (58%, both combined) but differed significantly among years at J. María. A higher percentage of nestlings reached fledging age at Arroyito (53%) than at J. María (42%). Mean number of young fledged per breeding pair was 2.2 at Arroyito and 1.4 (overall) at J. María (range: 0.5–2.3). The apparent preference exhibited by Monk Parakeets for nesting in eucalyptus trees against low native vegetation could be a result of the higher productivity of breeding pairs in the former habitat. The Monk Parakeet has a lower fledging and breeding success than other parrots. Due to its large clutch size, however, it has one of the largest productivities among psittacids. *Received 1 Aug. 1991, accepted 1 Feb. 1992.*

The Monk Parakeet's (*Myiopsitta monachus*) nesting habits are unique among psittacids. Whereas most parrots are hole or cavity nesters, this species builds large enclosed stick nests, which often are integrated in a compound nest that may include several isolated chambers (Forshaw 1978). These large communal nests closely resemble those of the Sociable Weaver (*Philetairus socius*) of Africa (Collias and Collias 1978). Unlike the majority of birds, Monk Parakeets occupy their nests throughout the year. During the non-breeding season, each nest chamber is inhabited by a variable number of individuals (juvenile and adults), whereas only a single breeding pair or two to three non-breeding birds occupy the nest in the breeding season (Martella 1985, Martín 1989). There is evidence suggesting that the social organization of this parakeet is complex (Martella 1985, Martín 1989) and has some characteristics of a communal breeder such as delayed breeding, reduced dispersal, and incipient helping (Bucher et al., in press). The Monk Parakeet is considered a pest throughout its range. Complaints include damage to crops (Bucher 1984) and to

[1] Centro de Zoología Aplicada, Univ. Nacional de Córdoba, Casilla de correo 122, 5000 Córdoba, Argentina.

artificial structures such as power lines (Bucher and Martin 1987). Control campaigns usually are based on direct killing without a proper understanding of the population dynamics of the Monk Parakeet. This may either make those control methods ineffective or eventually threaten the survival of this species. The Monk Parakeet is also exploited for the bird trade (Nilsson 1990).

In this paper, we present the results of a long-term study of the breeding biology of the Monk Parakeet. Besides providing general information on the subject, we discuss differences in reproductive output that may be associated with the apparent preference for nesting in eucalyptus compared to native trees.

STUDY AREAS AND METHODS

This study was conducted in two areas of Córdoba province, Argentina. One area was located at "San Antonio" ranch (31°25′S, 62°59′W), near the town of Arroyito, and the other was at "Los Leones" ranch (31°05′S, 64°11′W), close to the town of Jesus María. In both areas, the native vegetation has been cleared for agriculture and cattle-raising, leaving some interspersed remnants of the original xerophytic woodland. Mean annual rainfall at Arroyito is 700 mm and at J. María 870 mm (75% occurring between November and March). The daily temperature in both sites ranges from an average minimum of 4°C in July to a mean maximum of 30°C in January.

Our Monk Parakeet populations were studied from the pre-laying period (October) to post-fledging time (early March) at Arroyito in 1982 and at J. María from 1983 to 1988. In Arroyito, the studied nests were all grouped in rows of *Eucalyptus viminalis* trees planted at both sides of the 1000-m long ranch's entrance. In J. María, the nests were in native trees (*Celtis tala, Geoffroea decorticans, Aspidosperma quebrachoblanco* and *Prosopis* spp.) in a 610-ha study area where some nests were isolated and others were grouped. Because native trees do not grow as high as eucalyptus, nests at J. María were constructed below 10 m of height (roughly), whereas at Arroyito almost all nests were in higher locations.

In Arroyito, all accessible nests situated below 16 m in the first 400 m of the eucalyptus plantation were checked weekly with a cherry-picker. All eggs found were marked with a soft pencil, and the number of eggs and chicks was recorded on each visit. At J. María, all nests below a height of 6 m in the study area (about 70% of total) were inspected using a ladder at 10-day intervals on average (range 7–12). In this area, the eggs were marked individually with indelible ink, and after hatching, the chicks of the same nest initially were identified by clipping a different claw. From 1985 to 1987, nestlings were weighed (using Pesola spring scales) to the nearest 0.1 g for masses <10 g and to the nearest 1 g for chicks >10 g. In both areas nestlings were banded with numbered aluminum bands when they reached about 20 days old.

The date of clutch initiation was estimated for each nest chamber by back-dating, based on a 2.1-day interval between successive eggs and a 24-day incubation period (Navarro 1989). The age of nestlings, calculated by a growth curve equation (Navarro and Bucher 1990), was also used for back-dating when necessary. Although these methods provided accurate dating in most cases, there were some clutches in which no laying date could be estimated (e.g., found as a completed clutch with several eggs which did not hatch).

The fate of each egg was recorded as lost before hatching, failed to hatch, or hatched. Eggs that might have hatched but whose chicks disappeared before the following visit were

assumed not to have hatched. A juvenile was considered to have fledged when absent from the nest at ≥35 days after hatching. Disappearances at earlier ages were considered to be deaths. Causes of loss of eggs and chicks were assigned to (1) predation: eggs and chicks in nests in which there was evidence of predator attack (remains of mutilated carcasses) or there was a simultaneous loss of the whole nest's content without trace; (2) partial disappearance: vanishing of part of the clutch or brood, eggs falling from the nest, and a few cases when a total loss occurred after a partial loss; (3) failure to hatch: infertile eggs, death of the embryo, or desertion; (4) deaths in the nest: malnutrition, malformation, or sickness; (5) nest fall; and (6) manipulation.

First clutches refer here to the female's laying her first egg in the season; replacement clutches were those started following failure of the first clutch, and second clutches are those laid after a successful first brood.

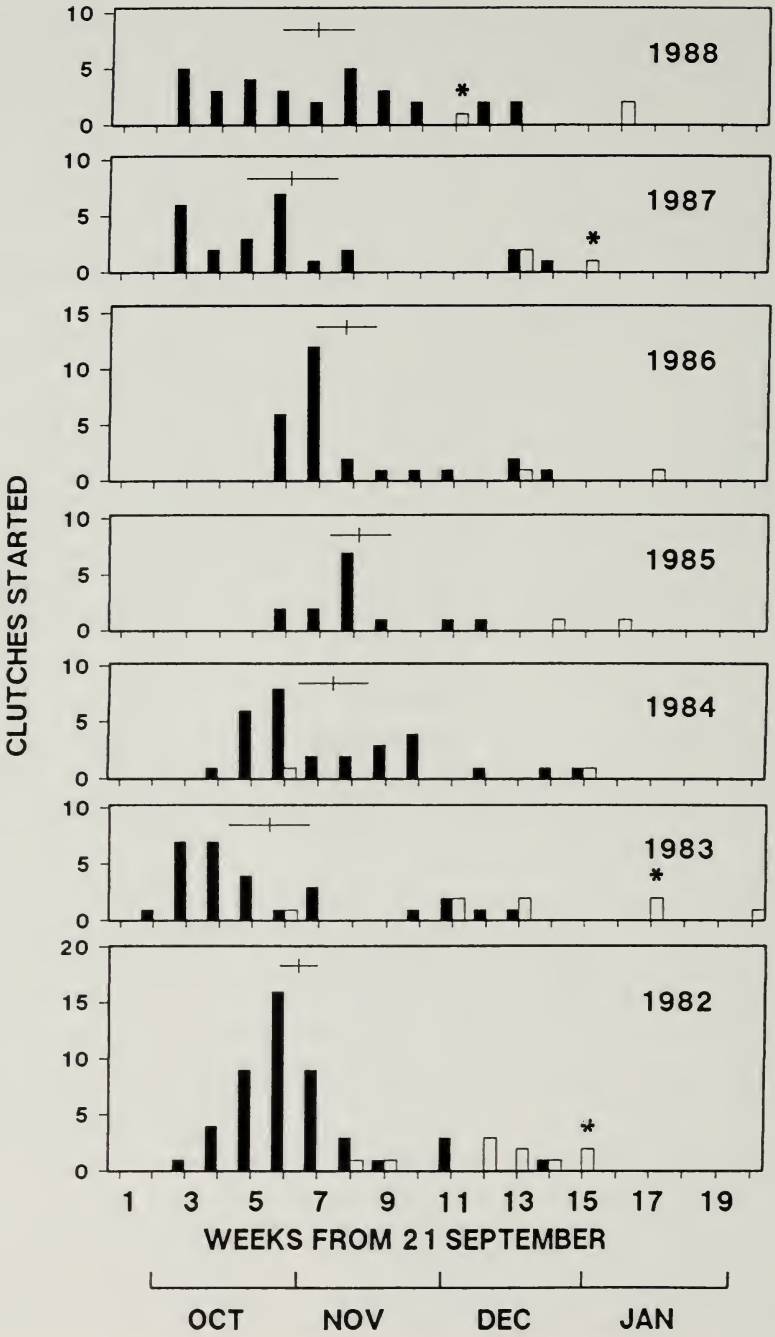
Given that periodic nest visitation has been reported as a factor that reduces nesting success in various avian species (Robert and Ralph 1975, Burtt and Tuttle 1983, Westmoreland and Best 1985), we attempted to evaluate the effect of the observers' disturbance on reproductive success by comparing the fledging recruitment in the studied population in J. María with that of undisturbed nests located in a 200-m-wide strip surrounding the study area. The reproductive output of both populations was measured from 1986 to 1988 by comparing the juvenile/adult ratio of birds in samples caught during the post-breeding season (mid-February to mid-March) using the nest trapping method described by Martella et al. (1987). The age class of all newly captured (unbanded) individuals was determined by the presence of remige molting (Navarro and Bucher, unpubl. data). We assumed that, at the time the samples were taken (late summer), dispersion had not yet taken place and that the juvenile/adult ratio would provide an unbiased estimation of overall productivity.

RESULTS

Compound nest size.—At Arroyito, 62% of the nests had only one chamber, 33% two, 5% one, and none had four. At Jesús María, proportions (all years grouped) were 73%, 19%, 6%, and 2%, respectively. Differences in percentages between areas were not significant (Chi-square test; $\chi^2 = 3.85$, df = 3, $P = 0.278$).

Timing of laying.—At Arroyito, mean clutch initiation date was 1 November (range: 12 October–21 December). In J. María, the overall mean was 5 November (range: 2 October–28 December). Yearly means at this site varied within a 19-day range from 26 October in 1983 to 14 November in 1985 (Fig. 1). The earliest initial egg laying was recorded on 1 October 1983 and the latest on 29 October 1985. Laying synchrony was highest in 1985 and 1986 (Fig. 1). The time-span required at both areas for the initiation of 90% of first clutches was almost nine weeks (from October to December). Throughout the study, 28 replacement clutches and five second clutches were laid from mid-November to early January at Arroyito and from late October to early February at J. María (Fig. 1).

Breeding attempts.—The percent of occupied nest chambers found with at least one egg differed significantly ($\chi^2 = 26.92$, df = 1, $P < 0.001$) between Arroyito (91%) and J. María (53% overall) (Table 1). At Arroyito,


1988
1987
1986
1985
1984
1983
1982
CLUTCHES STARTED
WEEKS FROM 21 SEPTEMBER
1 3 5 7 9 11 13 15 17 19
OCT NOV DEC JAN

35% of the breeding pairs that were not successful in fledging at least one chick with their first clutch began replacement clutches. At J. María, an overall 20% of unsuccessful pairs started replacement clutches. Neither the differences in percentage of replacement among years in J. María ($\chi^2 = 3.03$, df = 5, $P = 0.696$) nor between the two areas ($\chi^2 = 1.77$, df = 1, $P = 0.183$) were significant. Second clutches were rare, two being recorded in 1982 and one each in 1983, 1987, and 1988. This means that <2% of total breeding pairs each year began second clutches, and for all years, only 5% (5 of 99 cases) of those pairs that were successful with their first brood began second clutches.

Clutch size.—Mean number of eggs in first clutches at Arroyito (6.0 ± 0.24 eggs [SE]) was significantly different from that at J. María (overall mean 5.4 ± 0.13) (Mann-Whitney test; $Z = 3.27$, $P = 0.001$). Clutch sizes ranged from one to 11 eggs at Arroyito and one to nine eggs at J. María; in both sites >73% of clutches had five to seven eggs. Yearly means in J. María ranged from 6.1 ± 0.41 eggs in 1985 to 5.1 ± 0.24 in 1987. Mean clutch sizes were higher and fluctuated more from 1983 to 1985 than in later years; after a decline in 1986, they were relatively constant. However, differences among years in J. María were not significant (Kruskal-Wallis test; $Z = 9.57$, $P = 0.088$).

Non-first clutches (replacement and second clutches) were significantly smaller than the respective first clutches (Wilcoxon paired rank test; $Z = 2.89$, N = 33, $P = 0.004$). The mean difference between the first and the non-first clutch was 1.1 ± 0.34 eggs. Replacement (4.9 ± 0.21 eggs) and second clutches (4.0 ± 0.84) were not significantly different in size (Mann-Whitney test; $Z = 1.22$, $P = 0.221$).

Hatching success.—In Arroyito, 216 out of 373 (58%) eggs hatched, while at J. María overall hatching success was 55% (Table 1); the difference between areas was not significant ($\chi^2 = 0.69$, df = 1, $P = 0.408$). Discrepancies between years in J. María were significant ($\chi^2 = 19.90$, df = 5, $P = 0.001$) due to the presence of two years of high success (1986 and 1988) and one year of extremely low hatching success (1983) (Table 1).

Hatching success of replacement and second clutches was significantly lower than that of first clutches in both areas (Table 1) (Arroyito: $\chi^2 = 22.22$, df = 1, $P < 0.001$; J. María: $\chi^2 = 8.45$, df = 1, $P = 0.004$).

←

FIG. 1. Frequency distribution for Monk Parakeet clutch initiations at Arroyito (1982) and J. María (1983–1988). Mean first clutch initiation date (vertical lines) and its 95% confidence interval (horizontal lines) are plotted above each histogram. Unshaded bars indicate re-layings. Each asterisk represents the occurrence of a second clutch.

TABLE 1

BREEDING STATISTICS OF MONK PARAKEETS

Parameter	Arroyito	J. María					
	1982	1983	1984	1985	1986	1987	1988
Number of occupied nest chambers sampled	52	40	46	38	55	78	56
Percent chambers with eggs (% breeding pairs)	91	70	63	37	49	42	68
Number of eggs laid in first clutches	320	166	160	85	137	167	199
Mean size of first clutches	6.0	5.9	5.5	6.1	5.1	5.1	5.2
Hatching success (nestlings/eggs)	0.63	0.48	0.60	0.52	0.66	0.57	0.61
Fledging success (fledglings/nestlings)	0.55	0.08	0.40	0.36	0.63	0.55	0.42
Breeding success (fledglings/eggs)	0.35	0.04	0.24	0.19	0.42	0.32	0.26
Percent successful first clutches[a]	51	14	38	50	48	52	53
Percent of pairs re-laying[b]	21	29	10	14	11	9	8
Mean size of replacement/second clutches	4.8	5.1	4.3	5.0	4.0	4.3	5.0
Hatching success of replacement/second clutches	0.28	0.20	0.46	0.50	0.42	0.31	0.50
Fledging success of replacement/second clutches	0.20	0.41	0.33	0	1.0	0	0.80
Breeding success of replacement/second clutches	0.06	0.20	0.15	0	0.42	0	0.27
Percent successful replacement/second clutches[c]	9	25	33	0	67	0	67
Overall productivity per pair[d]	2.2	0.5	1.4	1.1	2.3	1.6	1.4
Overall productivity per occupied chamber[e]	2.0	0.4	0.9	0.4	1.1	0.7	1.0

[a] Clutches producing at least one fledging/breeding pair.
[b] Includes replacement and the following second clutches: 2 (1982), 1 (1983), 1 (1987), 1 (1988).
[c] Clutches producing at least one fledging/breeding pair that re-laid.
[d] Total fledglings produced/breeding pairs.
[e] Total fledgling produced/occupied chambers.

Differences in hatching success between replacement (26%) and second clutches (35%) were not significant ($\chi^2 = 1.22$, df = 1, $P = 0.270$).

Fledging and breeding success.—A significantly higher proportion (53% overall) of nestlings survived from hatching to fledging at Arroyito ($\chi^2 = 7.42$, df = 1, $P = 0.006$) than at J. María (Table 1). Overall fledging success at J. María ranged from 14% to 65%, with an average of 42%; differences among years were significant ($\chi^2 = 57.47$, df = 5; $P < 0.001$).

At Arroyito, fledging success of non-first clutches was significantly lower than first clutches ($\chi^2 = 5.61$, df = 1, $P = 0.018$); but no significant differences were found at J. María ($\chi^2 = 0.03$, df = 1, $P = 0.864$). Discrepancies between replacement (25%) and second clutches (35%) were not significant ($\chi^2 = 0.29$, df = 1, $P = 0.588$).

Significantly more eggs produced fledging young at Arroyito (27%) than at J. María (23% overall) ($\chi^2 = 7.76$, df = 1; $P = 0.005$).

Productivity.—Mean number of young fledged per breeding pair was 2.2 ± 0.32 at Arroyito. At J. María the overall mean was 1.4 ± 0.15, with yearly means ranging from 0.5 ± 0.24 in 1983 to 2.3 ± 0.48 in 1986. Although there was no significant difference in productivity between areas, the test was close to the significance level of 0.05 (Mann-Whitney test; $Z = 1.87$, N = 222, $P = 0.061$).

Significant differences were found among years in J. María (Kruskal-Wallis test; $Z = 12.33$, $P = 0.031$). The 1983 breeding season was notable for the comparatively high mean first clutch size and for being the one with the lowest productivity.

Reproductive success (proportion of females that successfully fledged at least one young) did not differ significantly between areas ($\chi^2 = 0.59$, df = 1, $P = 0.443$). However, in J. María the low success of 1983 lead to significant differences among years ($\chi^2 = 11.98$, df = 5, $P = 0.035$).

Causes of mortality.—The importance of different causes of loss varied significantly either among years at J. María ($\chi^2 = 180.66$, d.f. = 20, $P < 0.001$) or between study areas ($\chi^2 = 58.55$, df = 5, $P < 0.001$). Whereas percentage of losses due to predation, failure to hatch, and nest fall were slightly higher at Arroyito, deaths in the nest and partial losses were proportionally higher at J. María (Fig. 2). Overall, from 1982 to 1988, 23% of losses to the 1405 eggs laid was attributed to predation on eggs and chicks, 16% to partial disappearance; 16% to failure to hatch; 10% to deaths in the nest; 4% to nest fall; and less than 1% due to manipulation (only eggs were affected).

Circumstantial evidence for repeated predation by white-eared opossums (*Didelphis albiventris*) and grass snakes (*Philodryas patagoniensis*) was strong in both study areas (see also Martella and Bucher 1984, Martella et al. 1985). Both at Arroyito and J. María, two nests were attacked

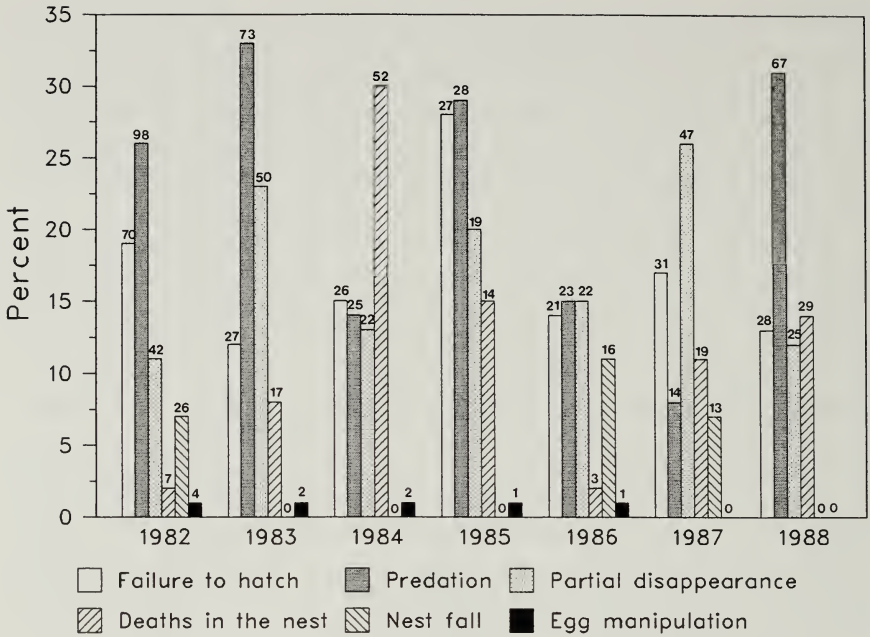


FIG. 2. Percentages of Monk Parakeet eggs and chicks lost with respect to the total number of eggs laid in that year. Values above bars are absolute frequencies.

and occupied by opossums. One night during early 1989, we observed an opossum that was trying to invade a Monk Parakeet nest. Also, in summer of 1983, we discovered a grass snake inside a nest as it was eating nestlings.

Effect of disturbance on reproductive outcome.—The overall juvenile/adult ratio determined in three post-breeding trapping opportunities at J. María (from 1986 to 1988) on the study area (0.40) did not differ significantly from the undisturbed area (0.37) ($\chi^2 = 0.03$, df = 1, $P = 0.865$), supporting the hypothesis that disturbance by observers did not affect breeding success.

DISCUSSION

Although the breeding season of the Monk Parakeet is restricted to spring and summer, and thus apparently controlled primarily by photoperiod, the average date of onset of breeding at J. María varied within a three-week period throughout the six monitored years (1983–1988). This slight shift in the dates of initiation of egg-laying may be related to other secondary environmental factors such as temperature, and food supply (Navarro and Bucher, unpubl. data). The Monk Parakeet has fewer year-

TABLE 2
COMPARISON OF BREEDING PARAMETERS AMONG THE MONK PARAKEET AND OTHER PSITTACIDS

Parameter	Monk Parakeet[a]	Australian parrots[b]	Cuban Parrot[g]
Clutch size	6	4[c]	3
Percent hatching success	56	70 (50–82)[d], 54[e]	46
Percent fledging success	45	53 (43–72)[d]	67
Percent breeding success	25	40[e]	31
Percent successful attempts	47	50 (35–66)[f], 63[e]	45
Juveniles fledged per breeding pair	1.5	1 (0.3–2)[d]	1
Nestling period (days)	35	37[c]	

[a] This study (unweighted mean, both areas combined).
[b] Average (range given in parentheses).
[c] Calculated for a body weight of 93 g using the equation of Saunders et al. (1984).
[d] Smith and Saunders (1986).
[e] Wyndham (1981).
[f] Saunders and Ingram (1987).
[g] Calculated from Gnam (1988).

to-year fluctuations than other psittacids from similar latitudes, such as Carnaby's Cockatoo (*Calyptorhynchus funereus latirostris*; Saunders and Ingram 1987) in Australia, which exhibits a five to seven-week range. On the other hand, our results show that Monk Parakeet populations are less synchronous in laying (nine weeks on average for the completion of first clutches) than those of most Australian parrots studied by Smith and Saunders (1986), the closest being the Red-tailed Black Cockatoo (*Calyptorhynchus magnificus*).

The clutch size of the Monk Parakeet is larger than that of most psittacids studied in detail (Table 2). This large clutch size counterbalances for the Monk Parakeet's lower fledging and breeding success (Table 2). A lower breeding success is consistent with the idea that the stick nest built by the Monk Parakeet, although safer than an open nest, is less secure than tree or cliff cavities. This issue may in turn have favored selection for a faster growth rate of nestlings (Navarro and Bucher 1990) and a shorter fledging period (Table 2).

An unexpected finding of our research is that a substantial and variable proportion of birds do not breed every year. Variations in the proportion of breeders modify the growth rate of Monk Parakeet populations through a change in the birth rate (Navarro and Bucher, unpubl. data). Therefore, an estimation of the fraction of breeders within the population should be used when developing demographic studies in parrots.

Although we found significant differences in some breeding parameters between Arroyito and J. María (particularly in percentage of chambers

with eggs and overall productivity per occupied chamber), comparison between the two areas must be made cautiously, given that we have data from only one breeding season and so lack information on annual variability in breeding statistics at Arroyito. Even if inconclusive, our findings suggest that the breeding performance of Monk Parakeets is better at Arroyito than at J. María. Possible hypotheses to explain this difference could be: (1) a higher quality or quantity of food sources at Arroyito; (2) eucalyptus trees are a better breeding habitat for this bird species than lower native vegetation; or (3) both factors combined.

Unfortunately, the lack of concurrent data on food supply at both study areas precludes us from testing the influence of this factor on productivity of Monk Parakeets.

Plantations of eucalyptus often enable higher densities of nests, which in turn could facilitate social interactions such as social stimulation, enhancement of foraging, and helping behavior, among others. Previous studies on the social organization of the Monk Parakeet revealed that such interactions appear to play a meaningful role in this higher gregarious bird species (Martella 1985; Bucher et al., in press.) and could yield a higher fitness. On the other hand, the predation rate was slightly higher at Arroyito, suggesting that neither nests in eucalyptus are safer than in lower vegetation nor that higher population densities would favor predator deterrence. However, human predation (e.g., pest control campaigns or harvesting of chicks for pet trade) should not be underrated as a cause of disturbance under normal circumstances. We do not evaluate here the importance of this factor, as it was restricted throughout our study. However, we think that Monk Parakeets often construct their nests as high as possible to reduce human disturbance.

Should we consider, therefore, eucalyptus as an optimal habitat for Monk Parakeets? Fretwell and Lucas (1969) defined optimal breeding habitats as those in which reproductive output is maximum, less-optimal habitats being selected only when density in optimal habitats is high enough to reduce fitness to a lower value than that observed in sub-optimal habitats. Accordingly, as the reproductive output was higher in eucalyptus trees, and assuming that habitat quality is somehow related to nest location, Monk Parakeets should construct the nest on eucalyptus trees wherever they are available. There is evidence confirming that this psittacid shows an apparent preference for nesting in eucalyptus or other tall trees or human structures (Bucher and Martin 1987) rather than lower native vegetation (Navarro, pers. obs.). This provides some support to Forshaw's (1978) argument that the introduction of eucalyptus trees has favored the distribution and abundance of the Monk Parakeet in the Pampas region.

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WINTER TERRITORIAL BEHAVIOR OF GRAY VIREOS

JOHN M. BATES[1]

ABSTRACT.—I studied a color-marked population of wintering Gray Vireos (*Vireo vicinior*) over two seasons (1985–1986 and 1986–1987) on study sites near Puerto Lobos, Sonora, Mexico. Some individuals had been banded as early as three years previously. Ten of 14 (71%) vireos banded in the winter of 1985–1986 returned to the same territories in the following winter. Territories were defended throughout the winter and averaged 0.9 ha in size. Territorial interactions occurred frequently along boundaries as neighbors trespassed to forage on each others' territories. Most birds appeared to defend individual territories, and both males and females probably held territories. *Received 2 July 1991, accepted 18 Dec. 1991.*

In a review of the literature on avian competition in the nonbreeding season, Greenberg (1986) noted that only a few studies had been carried out on territorial wintering birds over the entire winter season (Schwartz 1964, Myers et al. 1979, Rappole and Warner 1980, Greenberg 1986). Despite the lack of detailed studies, Greenberg suggested that territoriality is common among small insectivorous passerines in winter. Since Greenberg's review there have been several additional studies (Holmes et al. 1989, Ornat and Greenberg 1990), but we still lack basic data on demography and behavior of most insectivorous migrants in the nonbreeding season. Most information about vireos in winter is restricted to geographic distribution and habitat selection (Barlow 1980; but see Tramer and Kemp 1980, Greenberg, in press). The present study addresses aspects of territoriality and foraging behavior for Gray Vireos (*Vireo vicinior*) wintering along the coast of Sonora, Mexico. Data I present here include five seasons of banding data of which two include data on a group of color-banded wintering Gray Vireos.

Gray Vireos breed in open pinyon pine and juniper woodland and in the ecotone between this habitat and several types of lower elevation chaparral habitats from central Texas to California and Baja California and from southern Nevada and Utah to southern Arizona, southwestern Texas, and northern Coahuila, Mexico. Most Gray Vireos winter in the deserts surrounding the Gulf of California (A.O.U. 1983); however, there apparently is an isolated population of unknown size wintering in the Chisos Mountains of Texas (Barlow and Wauer 1971). Gray Vireos arrive on their wintering grounds in mid-September and remain through the end

[1] Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, Arizona 85721. (Current address: Museum of Natural Science and Dept. of Zoology and Physiology, Louisiana State Univ., Baton Rouge, Louisiana 70803.)

of April. Thus, most of these birds spend seven months of the year in a desert region that receives as little as 100 mm of rainfall annually.

STUDY SITES AND METHODS

The two study sites, Arroyo San Lorenzo (30°17′N, 112°48′W) and Cerro Prieto (30°19′N, 112°48′W) are south and north, respectively, of Puerto Lobos, Sonora, Mexico, on the eastern shore of the Gulf of California. The Puerto Lobos area is part of the Lower Colorado River Valley subdivision of the Sonoran Desert Scrub biome (Turner and Brown 1982), but the arroyos at the study sites share vegetational features with central Gulf Coast flora found farther to the south. These arroyos are dominated by "stem succulents," including two species of elephant tree (*Bursera hindsiana* and *B. microphylla*) and two species of columnar cacti (*Pachycereus pringlei* and *Lophocereus schottii*). Also common in the arroyos are jojoba (*Simmondsia chinensis*), sangre-de-drago (*Jatropha cuneata*), wolfberry (*Lycium* sp.), and ironwood (*Olneya tesota*). The surrounding hillsides are sparsely vegetated, primarily by creosotebush (*Larrea tridentata*) and white brittlebush (*Encelia farinosa*).

The study site at San Lorenzo is a desert arroyo (wash) roughly 2 km long and about 100 m wide that is the main drainage from a group of hills several km east of the coast. A large alluvial fan covered with teddy bear cholla (*Opuntia biglovi*) runs along much of the north edge of the site and steep canyon walls border much of the southern side. Searches conducted both upstream and downstream from the area revealed vireos in densities similar to those on the site. There are several small sparsely vegetated side canyons to the north and south where vireos also maintained territories. The much smaller Cerro Prieto site occupies a shallow drainage that runs along the base of an isolated volcanic hill into coastal dunes 0.5 km from the coast. On this site, all territories were in the main drainage. Although these study sites are about 10 km apart, they have similar vegetation and fauna, and for most aspects of the study, they have been considered together.

Field work was conducted on seventeen three-to-five-day trips to the study areas: four during winter 1985–1986 (first date of trips: 11 January, 27 February, 15 March, 4 April); 12 trips during the winter of 1986–1987 (first date: 5 September, 25 September, 2 October, 25 October, 10 November, 28 November, 11 December, 2 January, 12 January, 27 February, 18 March, 4 April) were during the winter of 1986–1987, and a return trip in 1988 (first date: 2 January).

In the first winter of the study, I tried to capture and mark as many vireos as possible. In contrast, during the 1986–1987 winter, mist netting was done on an irregular basis, usually to catch unbanded birds seen in certain areas and also to provide information on the movements of previously banded birds. All captured vireos were weighed, measured and banded with a unique three-color band combination and a U.S.F.W.S. aluminum band. During the winter of 1986–1987, 25 entire days and 22 half-days (296 h, 11 trips) were spent primarily gathering data on movements and other behaviors of individually marked birds. "Full" days were days when 100% of the daylight hours were spent on the study sites. On half-days, the morning or late afternoon hours were spent on the sites, but not both.

I mapped each study area by establishing one transect through each of the sites with stakes placed every 30 m. Plants and other features could be located relative to one another by pacing their perpendicular distance from the transect with the aid of a compass. Most of the time on the study sites was spent wandering through the sites in search of vireos. Whenever a vireo was encountered, either by sight or by vocalization, I attempted to identify it by color-band combination and follow it for as long as possible. Movements and positions of birds were noted in the field and plotted on study site maps. I determined territorial boundaries of the birds by mapping all movements observed for each bird. From these data,

TABLE 1
NUMBER OF RETURNING MARKED GRAY VIREOS TO TWO STUDY SITES IN SONORA, MEXICO, OVER SIX WINTERS

	Years after initial marking					
	1	2	3	4	5	6
Number marked	39	18	4[a]	4	3	2
Number resighted	18	11	4	3	2	1

[a] Seven birds banded first in the 1985–1986 winter were not followed after the 1987–1988 winter; thus it is not known whether or not they returned for a third winter.

I determined territory size as well. I made special note of areas where there were repeated confrontations between color-banded individuals. I also collected data on foraging, which is presented elsewhere (Bates, in press). Field data were dictated into a cassette recorder and later transcribed into field notebooks.

RESULTS

Banding data—S. M. Russell banded Gray Vireos and other species on the San Lorenzo study site for several days each spring, beginning in March of 1983 and continuing through March 1985. Of 39 Gray Vireos banded by Russell or me (including birds from Cerro Prieto) between March 1983 and the spring of 1987, 18 (46%) were observed or netted the winter following banding, and 11 of those 18 (61%) of marked birds that returned the first winter also returned the second year (Table 1). Because wintering Gray Vireos are difficult to observe or capture, and more than several days are required to detect all individuals at a site, these values are an underestimate of the actual return rate. This can be seen in the return data from the winters in which the sites were intensively studied.

From January through April, 1986, I color banded 14 birds on the two study sites. Ten of these 14 birds (71%) returned in the winter 1986–1987. An additional bird with an aluminum band was seen at the San Lorenzo site in January 1986 where in the 1986–1987 winter I caught and color banded a bird banded previously by Russell. Despite spending only four days on the sites in January 1988, I relocated eight color-banded birds. One of these birds was banded by Russell in March 1983, indicating that the bird was going through at least its sixth winter (Table 1) and had been captured or observed in the same area on the San Lorenzo site in all but one of these winters. Another individual also was banded in March 1983 and was spending its fifth winter on the sites in 1986–1987. Neither bird was found in the 1984–1985 winter, but this probably means they were not mist netted, not that they were not present (Russell pers. comm.).

During the 1986–1987 winter, some individuals were encountered only once or a few times, whereas other birds were seen repeatedly. No birds had arrived when I made the 5 September trip, but eight of 18 birds observed on the sites early in the season were seen on at least five of the 11 other trips. On some trips, an individual was not positively identified by color-band combination, but vocalizations were heard within the bird's territory. No individual bird was detected on all of the 11 trips due to the often secretive behavior of the species during the nonbreeding season and to the apparent departure of some individuals prior to April 2, when the last visit to the sites was made.

Evidence for territoriality—The behavior of wintering Gray Vireos can be defined as territoriality because the vireos actively exclude conspecifics from specific areas throughout the season. This active defense of an area against conspecifics distinguished territories from home ranges (Munger 1984). Neighboring birds were frequently seen in disputes that involved vocalizations and chases. These events occurred in the same areas throughout the winter. Disputes started when one bird was detected trespassing on another's territory. After a chase, one bird would usually give a trill that would be answered by the other. These trills are peculiar to Gray Vireos relative to other vireo species. The vocalization is almost never heard on the breeding grounds (pers. obs.), yet it is the most frequent vocalization on the wintering grounds (Bates 1987). The birds would square off across the same area each time. If the trills were close together along the boundary, one bird would usually move away from the boundary soon after the incident, and often, one or both birds would begin to sing. These types of interactions also occurred where other territories came together, and trilling and occasional singing were heard from two to three birds on adjacent territories throughout the winter. Pairs of trills given by one bird, and then another, and chases such as described above were also heard and seen along other territorial boundaries throughout the study sites, although in many cases flights of the birds and the dense vegetation prevented identification of the individuals involved.

Over the course of the winter, territories generally did not change, and behavior of birds seen outside what was thought to be their territories was different than behavior on the territory (see below). Territories appear to be stable from year-to-year, as all 11 color-banded birds that returned in the winter of 1986–1987 returned to areas that included the sites at which they were captured in the previous winter. This was also true of the eight color-banded individuals seen in January 1988. The two oldest banded birds on the site were seen or netted over at least five winters in the same parts of the San Lorenzo site (Russell, pers. comm.; Bates 1987).

Mean (±SD) territory size for Gray Vireos was 0.9 ± 0.36 ha (N = 9,

range = 0.3–1.4 ha). The distribution of vegetation in the arroyos caused vireo territories to be linearly arranged. Thus, some of the boundaries for each bird abutted unsuitable habitat such as the cholla-dominated fan to the north of the San Lorenzo site.

Movements of marked and unmarked birds.—During the 1986–1987 winter, one vireo netted in early October was not seen again; another was seen in October and November but not afterwards. Three other birds caught in the central portions of the study areas for the first time early in fall 1986 were seen again. One of these birds was seen throughout the winter. It defended a small portion of the main arroyo at San Lorenzo, and apparently expanded its territory to include more of the arroyo as the winter progressed. The other two birds appeared again on the Cerro Prieto study site on well-defined territories of other individuals in late March. In both cases the territory holder was not seen during late March. Considering the time of year and that one of the reappearing birds was singing from an exposed perch, the territorial bird had probably migrated from the study site. These birds may represent first-winter birds, but they may also represent older birds with territories off the study site.

In late September and October, unbanded birds on the sites are to be expected as birds arrive and territories are established. Once territories are re-established, unbanded birds should become less frequent. Only five sightings of unbanded birds on the main study areas were recorded from November to May 1987. These sightings are thought to represent four individuals, perhaps wandering birds seeking unoccupied areas, or trespassing birds from territories off the study sites. No influx of unbanded vireos was observed in the spring.

Evidence for trespassing.—Color-banded individuals were often observed crossing or having crossed into a neighbor's territory. On two occasions, I mist netted trespassing color-banded birds in the middle of territories adjacent to their own. Birds holding territories adjacent to one another would frequently enter each other's territory. When a bird reached the edge of its territory it would often continue foraging silently into the next territory until detected by the territorial holder. One bird penetrated as far as 70 m into a neighbor's territory. This behavior occurred throughout the winter. Trespassing did not seem attributable to ill-defined boundaries. Once a territorial bird detected a neighboring invader, a chase ensued followed by trills by one or both birds and often countersinging across an open area. This was repeated in the same area, with the birds even occupying the same two bushes on several different occasions. I have observed the same behavior in individuals wintering in similar habitat in the Sierra Pinta Mountains of southwestern Arizona 150 km north of Puerto Lobos.

Trespassers were silent and foraged inconspicuously in the densest vegetation available. The only trespassing bird I heard vocalize on a neighbor's territory was a bird in April on the territory of a neighbor that had already migrated. Gray Vireo behaviors such as those exhibited by trespassing neighbors match descriptions of behavior in wintering Hooded Warblers (*Wilsonia citrina*) considered to be nonterritorial or floating individuals (Rappole and Warner 1980). During the entire study, I observed only four individuals that may have been "floaters." My observations of Gray Vireos indicate that most aggressive interactions in the winter, even ones involving long chases, result from the detection of a trespassing neighbor, not a nonterritorial "floater." On two occasions, territory holders disappeared from the sites; however, this resulted not in a floating bird's gaining a territory, but in a neighbor's expanding its territory to include part of the unoccupied area.

DISCUSSION

Our knowledge of migrant birds on their wintering grounds is growing; however, with few exceptions (Myers et al. 1979, Price 1981) studies that have monitored wintering populations across the entire winter period have been limited to members of the Parulidae (Schwartz 1964, Rappole and Warner 1980, Holmes et al. 1989, Ornat and Greenberg 1990). Therefore, my description of Gray Vireo winter territorial behavior is an addition to this body of literature and can be compared to and contrasted with it.

Between-year site fidelity observed in Gray Vireos is similar to that described for Greenish Warblers (*Phylloscopus trochiloides*) in India (Price 1981). The 46% return rate for all banded Gray Vireos the year following banding and the 71% return rate for Gray Vireos banded in 1985–1986 are comparable to the 52% return rate for all Greenish Warblers Price studied, and a 67% return rate for Greenish Warblers returning to undisturbed habitat. Similarly, Nesbit and Medway (1972) reported a 63% return rate for Eastern Great Reed Warblers (*Acrocephalus orientalis*) in Malaysia. The overwinter site fidelity in the vireos is high, similar to that reported for Black-throated Blue Warblers (*Dendroica caerulescens*) wintering in Jamaica (Holmes et al. 1989), but not as high as that reported for American Redstarts (*Setophaga ruticilla*) in the same study.

Differences between Gray Vireos and other species are probably related to the vireos' unusual winter range and strong preference for wintering in coastal desert areas dominated by elephant trees (*Bursera microphylla*; Bates, in press). For Greenish Warblers (Price 1981) and for Northern Waterthrushes (*Seiurus noveboracensis*) in Venezuela (Schwartz 1964), individuals that had wintered farther south began migrating north through

areas with wintering populations before the local wintering individuals had departed. This pattern of movement was not seen in the vireos, perhaps because the birds have a relatively short migration route compared to those of the warblers and waterthrushes. There are very few records of either spring or fall migrant Gray Vireos away from known breeding or wintering localities.

Gray Vireos also defend larger winter territories than have been reported for other species. Price (1981) found Greenish Warbler territories to average only six trees, and Rappole and Warner (1980) reported the average territories of wintering Hooded Warblers and Wood Thrushes (*Hylocichla mustelina*) in tropical forest in Veracruz, Mexico, to be only 0.25 ha, or one-fourth that of the average Gray Vireo winter territory. Gray Vireo winter territories are still smaller than the 2.4 to 8 ha breeding territories reported for the species in central Arizona and Texas (Barlow 1978).

There is evidence that sexual segregation in the winter, as has been reported for some sexually dichromatic parulids (Lynch et al. 1985, Holmes et al. 1989, Ornat and Greenberg 1990), does not occur in monochromatic Gray Vireos. This suggests that vireos are similar to Greenish Warblers (Price 1981), another monochromatic species. Price found both male and female Greenish Warblers sang and held territories. Although I was unable to determine the sex of birds on my study sites, of eight Gray Vireo specimens (Univ. Arizona) collected in March from the same habitat at a site in Sonora, Mexico, 90 km south of Puerto Lobos, four are males and four are females, suggesting no segregation occurs in this portion of the species' winter range. Furthermore, Barlow and Wauer (1971) also reported collecting both males and females wintering in the Chisos Mountains, Texas. Thus, there is no evidence for sexual segregation in the nonbreeding season on a large geographic scale.

It is not known whether there might be behavioral dominance between sexes (or age classes) at a site as has been found in wintering American Redstarts (Holmes et al. 1989). J. C. Barlow (pers. comm.) suggests that only male Gray Vireos respond by singing to playback of recorded songs in winter. If this is true, then most of the individuals that I followed for extended periods of time were males (although no individuals on the study sites responded consistently to playbacks of recorded songs). Two birds that were never heard singing despite being seen regularly throughout the study, may therefore have been females. These birds also had small territories (0.3 and 0.6 ha).

The trespassing behavior of the vireos is similar to that described for "floating" Hooded Warblers wintering in Mexico (Rappole and Warner 1980). These authors cited three reasons indicating that there were a substantial number of nonterritorial individuals, or floaters, on their sites

in southern Mexico (1) These individuals were captured throughout the winter on other birds' territories; (2) These individuals took over territories of occupants given the opportunity; and (3) Movement and other behaviors of these individuals were different from those of territory owners. All three of these traits were exhibited by territory-holding neighbors in my study, suggesting that an individual on another bird's winter territory is not necessarily a floater.

Two hypotheses might explain the high frequency of trespassing that I observed in Gray Vireos. First, trespassing may allow a bird to obtain additional resources at little cost, without depleting the ones that it defends. The other is that trespassing may be a challenge to a neighboring bird, testing whether that neighbor is capable of defending its territory. This may be especially true near the end of the winter, when birds were observed foraging and even singing on adjacent territories recently vacated by birds that had apparently left the study area. Trespassing does not undermine the adaptive nature of territoriality. Although a cost of leaving a territory to trespass is that another bird may forage on the undefended resources (for the vireos this is fruit of *B. microphylla* and insects; Bates, in press) of the trespasser, earlier defense of a territory probably deters some usage of those resources by another individual even without the physical presence of the defender. The trespasser benefits immediately in terms of depleting a resource that it does not defend, and it may also gain information about resources in areas that might become vacant in the future.

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STATUS, NESTING DENSITY, AND MACROHABITAT SELECTION OF RED-SHOULDERED HAWKS IN NORTHERN NEW JERSEY

THOMAS BOSAKOWSKI,[1] DWIGHT G. SMITH,[2] AND ROBERT SPEISER[3]

ABSTRACT.—Response rates of Red-shouldered Hawks (*Buteo lineatus*) and Red-tailed Hawks (*B. jamaicensis*) to broadcast vocalizations in suitable/marginal Red-shouldered Hawk habitat indicated that the species was not completely isolated by habitat. Red-shouldered Hawk responses were not dependent on the time of day, but occurred more frequently near larger wetlands (>10 ha). Sixteen active nests were found in a 7200-ha survey area representing the densest nesting population reported (0.22 nests/100 ha). Macrohabitats of 14 Red-shouldered Hawk nest sites were compared to 64 unused sites. Results revealed preferences for wetlands, stream bottomlands, small forest openings (owing to wetlands), and coniferous and mixed forest habitats but avoidance of suburban, open water, and deciduous forest habitats. *Received 30 July 1991, accepted 12 Jan. 1992.*

Significant declines of Red-shouldered Hawks (*Buteo lineatus*) on Breeding Bird Survey routes have been observed in the Northeast (reviewed by Titus et al. 1989). Hawk migration data also indicate a significant long-term decline in their numbers from 1946 to 1986 (Bednarz et al. 1990). Several northeastern states have responded to regional declines in nesting populations by listing the species as "threatened" (New York, New Jersey), of "special concern" (New Hampshire, Maryland), or as a candidate for listing (Pennsylvania) (Titus et al. 1989). In New Jersey, the species status has recently been upgraded from threatened to endangered. Studies have shown that nesting Red-tailed Hawks (*B. jamaicensis*) will displace Red-shouldered Hawks when thinning reduces canopy closure and crown volumes of mature stands (Bryant 1986). Recent studies of the Craighead's (1956) study area in Michigan have documented a complete displacement of the Red-shouldered Hawk by the larger and more aggressive Red-tailed Hawk during the 1970s and 1980s (S. Postupalsky, pers. comm.).

In northern New Jersey, we have observed that the majority of the Red-shouldered Hawk nesting population occurs in a small region, the Northern Highlands, where forest fragmentation and urbanization are still limited. The purpose of this investigation was to locate existing nesting territories, determine essential habitat requirements, and determine factors that may affect the current distribution of the Red-shouldered Hawk.

[1] Dept. of Biological Sciences, Rutgers Univ., Newark, New Jersey 07102. (Present address: Utah Div. Wildlife Resources, 1465 West 200 North, Logan, Utah 84321-6262.)
[2] Biology Dept., Southern Connecticut State Univ., New Haven, Connecticut 06515.
[3] 13 Beam Place, Haledon, New Jersey 07508.

STUDY AREA

We surveyed the Northern Highlands region of northern New Jersey, north of Routes 80 and 15 to the state line. This area includes Morris, western Passaic, eastern Sussex, and western Bergen counties. Speiser and Bosakowski (1987, 1988) provide a complete description of the study area's forest vegetation and physiognomy. Briefly, the Highlands is extensively forested, with sporadic human developments, mostly suburban. Forests are mostly mature second-growth deciduous forest dominated by oaks (*Quercus* spp.); old-growth forest is extremely rare. Pockets of coniferous growth, including eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*), frequently occur along water courses, around wetlands, or in areas with moist, humic soils.

METHODS

Broadcast surveys.—The survey period for the study was from 28 March to 29 June 1990. The intent of the survey was to find as many breeding Red-shouldered Hawks as possible, but no effort was made to cover systematically the entire study area. Therefore, we used wetland-biased survey sites which were limited to suitable breeding habitat: mature forested wetlands, beaver meadows, and mesic lowland forests. We surveyed nearly all suitable wetlands in the study area (>80%) except for a few extremely remote sites or sites where we could not gain permission to enter property.

Tape-recorded vocalizations of Red-shouldered and Red-tailed hawks were broadcast at 151 sites, including 17 sites which were repeated along (<400 m) the same wetland body. Tapes were broadcast from a portable cassette-deck (Contec Model V83, Japan) at nearly full volume (10 watt output) but with minimal distortion. The unit had two detachable speakers which were mounted back-to-back and hung from available tree branches about 1.5 m from the ground. The tape started with a 30-sec silent period to allow the investigators to seek a concealed position about 20–30 m from the speakers. After the initial silent period, Red-shouldered Hawk vocalizations continued for a 3-min period followed by a 3-min period of silence, and then a 3-min period of Red-tailed Hawk vocalizations.

If Red-shouldered Hawks responded to the first portion of the tape, the Red-tailed Hawk segment was not broadcast in order to avoid further alarm to the residents. If Red-shouldered Hawks responded during the Red-tailed Hawk broadcast, the tape was immediately stopped. At each site, we recorded the time of the start of taped vocalizations and the time of first response. We also recorded the number of birds responding, their sex and age if possible, direction and distance of first response, and the type of response (audio, visual, or both).

Nest searches.—After a positive response, nest searches were initiated in most cases except on private property. We also investigated previously used nests (traditional nest sites) for signs of nesting activity (greenery, incubating females, or protesting males). If the old nest did not show signs of recent activity, a thorough foot search of the area was conducted to look for new nests. A special effort was made to find all active nests in an intensive study area (7200 ha). This area included Wawayanda State Park and the northern Pequannock Watershed where previous field studies (Bosakowski 1990, Speiser, unpubl. data) suggested a high density of nests.

Macrohabitat analysis.—A macrohabitat analysis was performed on 14 nests sites and 64 unused sites in the southern end of the intensive study area where aerial photographs were available. The unused sites were defined as broadcast sites where no Red-shouldered Hawk response were obtained during a 1989 broadcast survey of 11 raptor species (Bosakowski 1990) or where no previous sightings or nests were observed during breeding-bird surveys in 1986–1987 (Benzinger et al. 1988).

At each site, habitat was evaluated within a 300 m radius using winter 1982 aerial

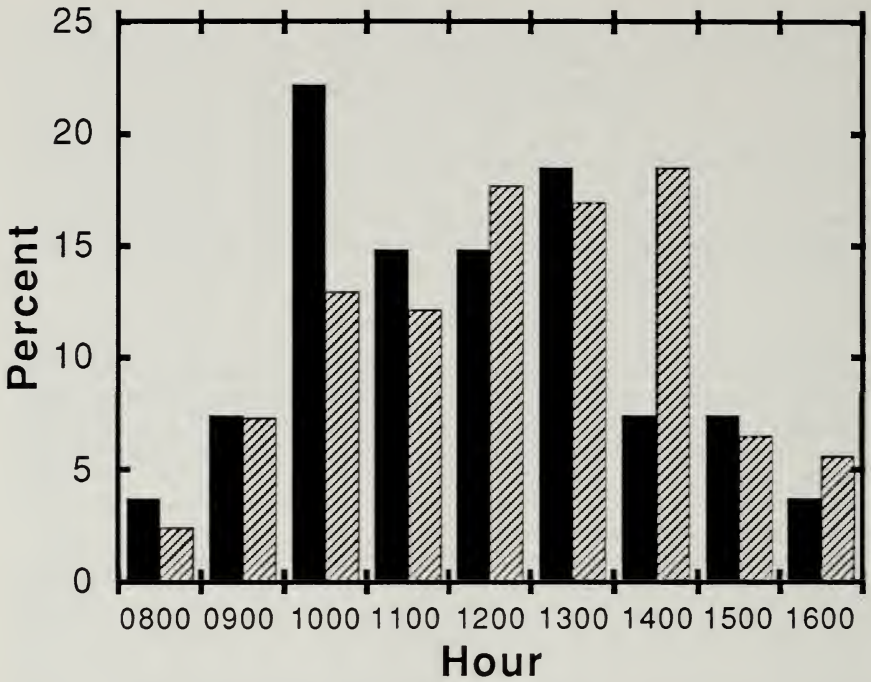

FIG. 1. Hourly response rates of Red-shouldered Hawks to broadcasts of tape-recorded calls during the breeding season. (Black bars = response, N = 27; hatched bars = no response, N = 124.)

photographs (1:8000). Seven macrohabitat types were recognized from aerial photographs, and the areas of each within the habitat circle were measured with a dot grid counter overlay sheet. The length of paved roads and forest edge within the habitat circle were overlayed with a fine thread and measured. Distances to the nearest forest opening larger than 0.5 ha, paved roads, human habitation, streams, lake/ponds (>0.5 ha), and wetlands (>0.5 ha) were measured from aerial photographs. USGS topographic maps were used to determine elevation (±5 m), slope (maximum rise in elevation over a 300 m baseline), and slope location (qualitative ranking: no slope = 0, lower slope = 1, middle slope = 2, and upper slope = 3, after Speiser and Bosakowski 1988). An index of topographic relief was measured as the number of isolines intercepted by 300 m radii in each of the four cardinal directions.

Statistical analysis.—Non-parametric univariate testing was used to compare the 21 macrohabitat variables of nest sites against unused sites. For this purpose, Mann-Whitney *U*-test was applied since non-normal, percentage, and rank data do not require transformations prior to analysis (Zar 1974).

Stepwise discriminant function analysis (DFA) was used to determine how well the variables chosen could discriminate between nest sites versus unused sites. This is determined by a postpriori reclassification procedure (Kachigan 1989) of nest sites and unused sites based on their individual scores from the discriminant function equation. A principal components analysis (PCA) was also run on the data to reveal the most important factors or combination of factors in nest-site selection. This type of analysis reduces a large number

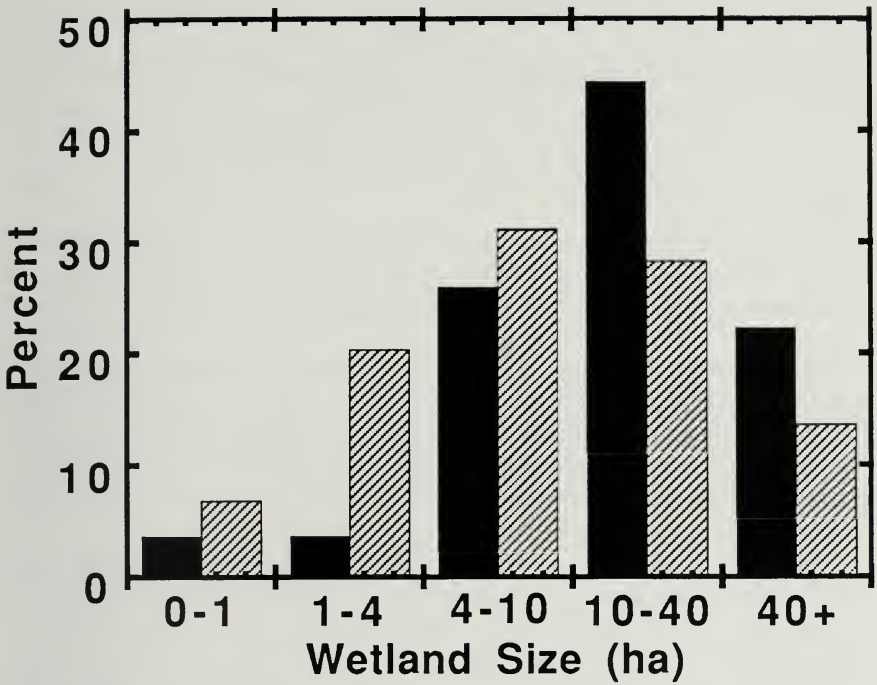

FIG. 2. Response rates of Red-shouldered Hawks to broadcasts relative to wetland size. (Black bars = response, N = 27; hatched bars = no response, N = 103.)

of variables into a smaller number of related factors (Kachigan 1989) which may be useful in identifying significant features of selected habitats.

The multivariate tests were run on a VAX mainframe computer using SPSSx software (SPSS 1988, Norusis 1985), which standardizes all data entries prior to analysis (SPSS 1988). Data reduction procedures were used to remove redundant or highly correlated ($r > 0.7$) variables prior to application of multivariate methods (Green 1979). The variable removed was one of each pair of highly correlated variables that was least interpretable in an ecological sense (Titus and Mosher 1981). Mahalonobis distance was used to standardize data for the discriminant function analysis (SPSS 1988).

RESULTS

Survey response.—Twenty-seven Red-shouldered Hawks responded out of a total of 151 broadcasts. No significant effect of time of day on response rate was found (Fig. 1). Although an overall Chi-square analysis could not be performed because of some low cell frequencies (Zar 1974), the largest differences at 10:00 and 14:00 were not significantly different when tested with Fisher's Exact Test ($P = 0.23$, $P = 0.5$, respectively).

Red-shouldered Hawk responses were classified with regard to the size of the nearest wetland (Fig. 2). Data from additional unused sites along

the same wetland body were not included so that the sample size from unused sites is smaller than shown in Fig. 1. A higher ratio of response versus no response by Red-shouldered Hawks occurred in the two largest wetland classes. When the data were pooled into two wetland groups (<10 ha, >10 ha), the percent responses were significantly different (Fisher Exact Test, two-tailed, $P = 0.03$) with a greater response in the larger wetland class.

Red-tailed Hawks responded less frequently (9/112 = 8.0%) compared to Red-shouldered Hawks (27/133 = 20.3%). Spatially, the two species overlapped only at three sites, and heterospecific aggression was observed once.

Including responses made prior to broadcasts and sightings made from extensive foot surveys for nest sites, a total of 61 contacts with Red-shouldered Hawks were made during the study. Eliminating repeat sightings near or on nests, there were 37 different locations which included 17 active nests. Sixteen of the active nests were found in the intensive study area giving a nesting density of 0.22 nests/100 ha.

Macrohabitat selection.—Analysis of 14 Red-shouldered Hawk nest sites revealed that they were located significantly farther from roads and human habitations than unused sites (Table 1). The number of houses within habitat circles around nests tended to be lower than unused sites, but the mean was inflated because one nest had an unusually large number of houses (47). Of the remaining 13 nests, 12 had no houses within the 300-m radius circles. Similarly, nest sites generally had a lower percentage of suburban area than at unused sites, but the mean value was inflated by two outlying nest sites. Road length traversing the habitat circles generally was shorter in Red-shouldered Hawk sites, but the number of roads did not differ significantly from unused sites.

Red-shouldered Hawk nests were significantly closer to wetlands and streams, but not to lakes and forest openings, than were unused sites. Edge length did not differ from that of unused sites. Land cover at Red-shouldered Hawk nests was characterized by significantly greater amounts of wetland, coniferous forest, and mixed forest, and significantly less deciduous forest and less suburban area (lower rank; data not shown in Table 1). Field and open water habitats were not different between groups. Topographically, nests were placed at significantly lower slope locations than unused sites, but overall relief and percent slope did not differ significantly. Nest sites occurred at significantly higher elevations than unused sites.

After data procedures (described in Methods), 16 remaining variables were entered into a stepwise DFA. The analysis reduced the discriminant function into a nine-variable equation (Table 2) which was able to cor-

TABLE 1

MACROHABITAT AT 14 RED-SHOULDERED HAWK NESTS AND 64 UNUSED SITES IN THE INTENSIVE STUDY AREA[a]

Variables	Nest sites (N = 14)	Unused sites (N = 64)	*P* level
Distance to road (m)	812 ± 634	348 ± 304	0.0042*
Distance to human hab. (m)	1013 ± 614	529 ± 468	0.0051*
Distance to stream (m)	64.5 ± 49.9	176 ± 149	0.0021*
Distance to lake (m)	633 ± 308	499 ± 352	0.1798
Distance to wetland (m)	61.3 ± 43.5	436 ± 451	0.0001*
Distance to opening (m)	97.3 ± 61.4	210 ± 200	0.1091
Number of roads	0.57 ± 1.34	0.78 ± 0.97	0.1085
Road length (m)	142 ± 274	320 ± 416	0.0844
Number of houses	3.64 ± 12.5	2.70 ± 5.03	0.0676
Edge length (m)	434 ± 406	538 ± 553	0.7907
Suburban (%)	2.0 ± 6.5	1.9 ± 3.1	0.0595
Field (%)	0.7 ± 1.3	2.7 ± 4.5	0.1584
Wetland (%)	16.0 ± 6.3	5.3± 6.7	0.0001*
Coniferous forest (%)	14.3 ± 19.6	6.3 ± 7.8	0.0488*
Mixed forest (%)	43.3 ± 23.4	9.2 ± 8.7	0.0001*
Deciduous forest (%)	23.6 ± 20.9	69.0 ± 18.6	0.0001*
Open water (%)	0.8 ± 1.3	4.1 ± 8.0	0.5973
Elevation (m)	362.7 ± 128.0	307.1 ± 48.9	0.0001*
Slope (%)	5.3 ± 3.8	6.8 ± 5.2	0.3514
Slope location (0–3)	0.36 ± 0.63	1.25 ± 1.00	0.0017*
Relief (no. of isolines)	11.6 ± 3.0	14.6 ± 6.70	0.1190

[a] Data represent the mean ± SD.
* Difference significant at least at $P < 0.05$ level as determined by two-tailed Mann-Whitney *U*-test.

rectly identify 13 of the 14 nests sites (92.9%) and 100% of the unused sites. The overall correct classification rate was 98.2%, with no unused sites incorrectly classified as nest sites.

A PCA resulted in six factors which explained 70% of the variation in the data set (Table 3). The sixth factor was included since it was only slightly below the normal cut-off eigenvalue of 1.0 (Kachigan 1989) and was explained almost entirely by a single, easily interpreted variable.

The first factor (PC1) had highest correlations with distance to paved roads, distance to human habitation, suburban area, elevation, and mixed forest. PC1 represents a habitat gradient from suburban to wilderness (Fig. 3). The inclusion of mixed forest and elevation is the result of their correlations with remote, undeveloped areas in the study area. This gradient indicates that Red-shouldered Hawks tend to nest in areas with a general absence of human disturbance. The second factor (PC2) had highest correlations with distance to wetlands, wetland area, and slope rep-

TABLE 2

SUMMARY OF A STEPWISE DISCRIMINANT FUNCTION ANALYSIS OF MACROHABITAT AT 14 RED-SHOULDERED HAWK NEST SITES AND 64 UNUSED SITES

Final variables[a]	Standardized canonical coefficient
(a) Dist. human habitation	0.193
(b) Dist. stream	−0.154
(c) Dist. wetland	0.363
(d) Suburban area	0.294
(e) Field area	−0.166
(f) Wetland area	0.756
(g) Coniferous forest area	0.366
(h) Mixed forest area	0.829
(i) Elevation	0.403

Discriminant function equation[a]

DF I = a(0.000388) + b(−0.00112) + c(0.000883)
+ d(0.0754) + e(−0.0405) + f(0.114)
+ g(0.0339) + h(0.0662) + i(0.00274) − 5.390

Group centroids:

Nest sites = 3.546
Unused sites = −0.776

Group cut-off score = 2.161

[a] Variables a to i are each weighted by unstandardized canonical coefficients in parentheses.

resenting a habitat gradient from flat wetlands to steep uplands (Fig. 3). Along this axis, Red-shouldered Hawk nest sites were sharply skewed toward the wetland end of the gradient.

The third factor (PC3) had highest correlations with distance to openings, edge length, and field area. Nest sites were centrally located along this gradient compared to unused sites not favoring either extreme of the unused sites. The fourth factor (PC4) had highest correlations with distance to lake/pond and open water area. Nest sites were moderately skewed away from open water environs. The fifth factor (PC5) had highest correlations with distance to stream and slope location with nest sites conspicuously skewed toward bottomland-stream environments. The sixth factor (PC6) had a single very high correlation with coniferous forest area. Along this axis, only some nests sites were sharply skewed towards coniferous areas, but it should be noted that this category was not inclusive of mixed forest.

DISCUSSION

Survey responses.—Red-shouldered Hawks responded to broadcasts at all hours surveyed from 08:00 to 16:00 EST and no significant differences

TABLE 3

SUMMARY STATISTICS OF A PRINCIPAL COMPONENTS ANALYSIS (PCA) OF MACROHABITAT AT 14 RED-SHOULDERED HAWK NESTS AND 64 UNUSED SITES. HIGHEST FACTOR LOADING FOR EACH VARIABLE IS UNDERLINED FOR THAT FACTOR

Statistics[a]	Principal component factors					
	1	2	3	4	5	6
Eigenvalue	3.29	2.68	2.02	1.27	1.01	0.93
Percent of variance	20.6	16.8	12.6	7.9	6.3	5.9
Cumulative percent	20.6	37.4	50.1	58.0	64.3	70.2
Variables	Varimax-rotated factor loadings					
Distance to road	0.788	−0.129	−0.020	0.140	−0.137	−0.270
Distance to human	0.854	−0.027	0.076	−0.146	−0.063	0.102
Distance to stream	−0.028	0.065	−0.845	−0.012	0.873	−0.068
Distance to lake	0.030	−0.043	−0.034	0.822	0.115	0.094
Distance to wetland	−0.162	0.824	0.246	0.114	0.046	−0.145
Distance to opening	−0.001	0.432	−0.693	0.216	0.210	−0.163
Edge length	−0.056	−0.008	0.799	−0.270	−0.108	0.113
Suburban percent	−0.592	−0.195	0.146	0.101	−0.021	−0.068
Field percent	−0.204	0.149	0.799	0.046	0.168	−0.075
Wetland percent	0.162	−0.760	0.078	0.091	−0.286	−0.027
Coniferous percent	0.035	−0.063	0.091	0.126	−0.031	0.949
Mixed percent	0.491	−0.293	−0.003	0.341	−0.205	0.102
Open water percent	0.074	0.025	0.295	−0.820	0.174	−0.016
Elevation	0.685	−0.175	−0.245	0.043	0.125	0.041
Slope %	0.212	0.572	−0.279	−0.232	0.110	0.047
Slope location	−0.051	0.404	0.061	−0.025	0.739	0.057
Group mean factor scores						
Nest sites	0.999	−0.857	0.037	0.533	−0.581	0.394
Unused sites	−0.215	0.185	−0.008	−0.115	0.125	−0.110

[a] Note some variables have been eliminated prior to analysis because of high collinearity (cf Methods).

in time of day were found. However, we purposely avoided broadcasting at earlier or later hours because of diminished levels of thermals at these times.

Response rate increased near larger wetlands, thus suggesting that wetland size appears to be an important component of habitat suitability. Bednarz and Dinsmore (1982) recommended Landsat data to identify potential breeding habitat for Red-shouldered Hawk surveys (0.7% of Iowa), rather than random statewide surveys. The results from this survey show that wetland-biased point samples increased detection rates over random transect counts made in New York, Connecticut, and Wisconsin, but not Maryland (Mosher et al. 1990). Thus, the habitat-biased method may be more desirable for the purpose of a status survey, especially if

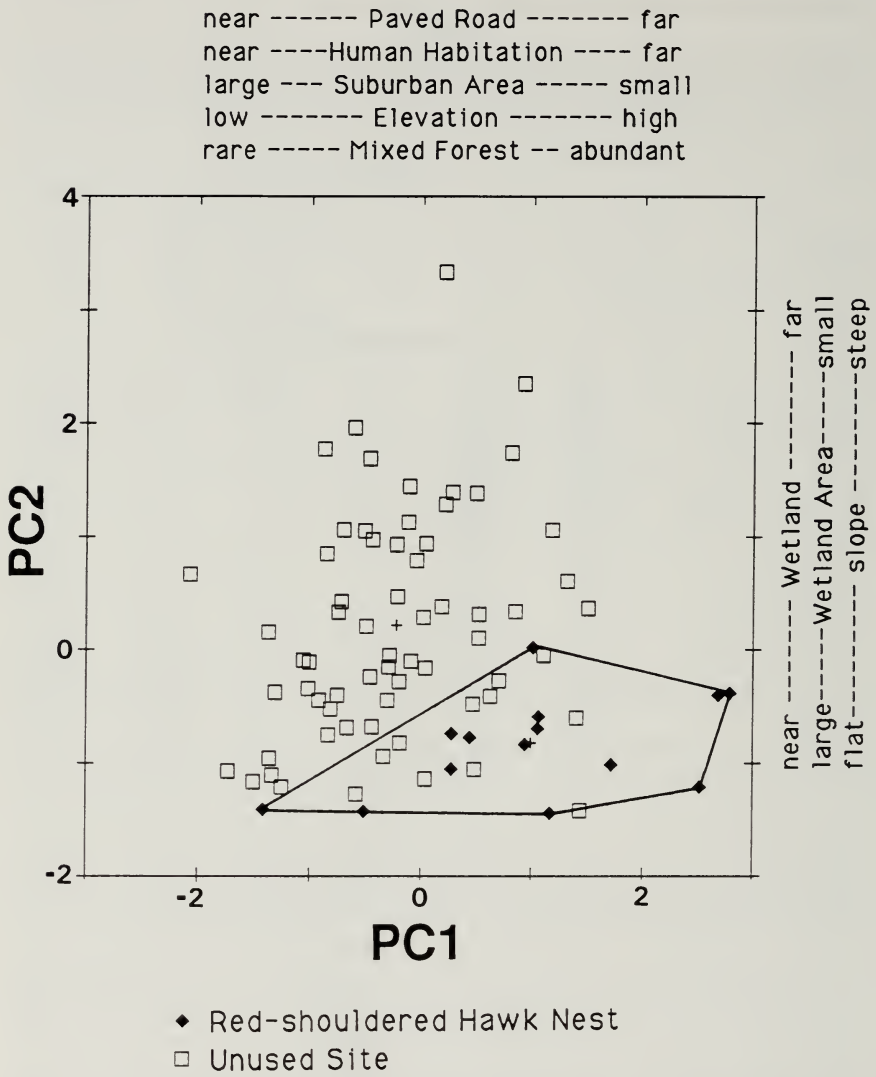

FIG. 3. Two-dimensional plot of principal component scores for macrohabitat of 14 Red-shouldered Hawk nest sites and 64 unused sites along PCA gradients 1 and 2. (+ indicates group centroids.)

field time is limited or the Red-shouldered Hawks are too rare to make random detection efforts worthwhile.

Response rate by Red-shouldered Hawks were greater than Red-tailed Hawks in the wetland-biased survey sites, but the occurrence of both

species indicates that they are not completely isolated by habitat partitioning. While spatial overlap of these congeners is generally found to be small (Craighead and Craighead 1956, Sharp and Campbell 1982) or nonexistent (Bosakowski 1990), negative distributions can often represent evidence for competition (Begon et al. 1986). We argue that a small amount of territorial displacement each year could result concomitantly with habitat degradation, thus inducing a chronic, long-term decline of the Red-shouldered Hawk. Moreover, many northeastern states have shown recent increases in breeding Red-tailed Hawk populations (Titus et al. 1989).

Population status.—Nesting density in the intensive study area was 0.22 nests/100 ha, which was substantially higher than the nesting density (0.10 nests/100 ha) reported by the Craighead's (1956) in Michigan farmland (only 11% wooded). Stewart (1949) reported a nesting density of 0.09 nests/100 ha and a territory density of 0.11 pairs/100 ha in Maryland. Henny et al. (1973) studied Stewart's (1949) population but density figures were not comparable since they included only area of river floodplain in their density calculations. To our knowledge, the intensive study area contains the densest population of nesting Red-shouldered Hawks reported to date.

Macrohabitat selection.—Red-shouldered Hawks nested in areas near larger wetlands, closer to streams, and had lower slope locations than unused sites. These preferences confirm wetlands as an important habitat in this region and elsewhere. Bednarz and Dinsmore (1981, 1982, 1985) found nesting Red-shouldered Hawks restricted to river floodplain and bottomland forest in Iowa. Henny et al. (1973) reported on a population nesting along a river floodplain in Maryland, and most Red-shouldered Hawk nests in Arkansas were in floodplain forest or close to water (Preston et al. 1989). In southeastern Missouri, Kimmel and Fredrickson (1981) found 13 of 14 nests in bottomland hardwoods. Portnoy and Dodge (1979) reported on a population occurring in wet deciduous woodland in Massachusetts. Titus and Mosher (1981), Sharp and Campbell (1982), and Morris and Lemon (1983) did not mention positive or negative associations of nest sites and wetlands in Maryland, Ontario, and Quebec, respectively. While the importance of wetlands may vary regionally in response to other variables, the great majority of studies have shown this species to be strongly associated with wetland habitats.

Red-shouldered Hawks in this study also nested in areas having greater proportions of coniferous and mixed forest than expected. A correlation with coniferous growth has been noted previously only by Sharp and Campbell (1982), albeit most studies have been conducted in deciduous forests. We hypothesize that the apparent preference for coniferous forest

could be somewhat correlated with the mesic and/or acidic soils of wetlands that are often dominated by eastern hemlock and white pine. Other possible reasons could be that these dense canopied stands may be too thick for nesting by Red-tailed Hawks or may provide concealment from Great Horned Owl (*Bubo virginianus*) predation (Bosakowski et al. 1989).

Few studies have included an analysis of variables which result from encroaching civilization. Bednarz and Dinsmore (1982) found that Red-shouldered Hawks nested significantly farther from buildings than Red-tailed Hawks in Iowa. Interestingly, their mean distance to buildings for Red-shouldered Hawk nests (1001 m) is nearly identical to that of our study region. Armstrong and Euler (1982) observed Red-shouldered Hawks significantly less near lakeshore areas with cottage development, compared to Broad-winged Hawks. Robbins et al. (1989) suggest that the Red-shouldered Hawk is an area-sensitive forest species. Our results show a strong avoidance of development (houses, paved roads) and other factors associated with smaller, fragmented forest tracts (Lovejoy et al. 1986). Bednarz and Dinsmore (1982) and Sharp and Campbell (1982) speculated that development, timber cutting, drainage alteration, and shooting near farms were the most serious threats to Red-shouldered Hawk populations.

Multivariate habitat analysis and management applications.—The DFA results showed that the macrohabitat variables measured in this investigation were extremely accurate in predicting nest sites or unused sites (98.2% classification accuracy). These results demonstrate the importance of macrohabitat for forest-nesting raptors. Bosakowski (1990) has recently reported that forest macrohabitat features can result in equal or even better classification rates than when only forest microhabitat variables (e.g., basal area, stem densities, canopy cover) are used. Furthermore, the latter methods require labor intensive on-site field efforts while macrohabitat can be determined directly from aerial photographs and topographic maps.

The task of measuring maps for future habitat management can be reduced dramatically by applying a stepwise DFA. For example, the 21 original variables measured in our study were reduced to nine variables with a minimal loss of precision for predicting habitat use. Potential habitat could be identified by using site data for the nine variables of the discriminant equation and determining its discriminant score relative to the group cut-off score (Kachigan 1989). Alternately, the PCA results could be used by selecting an important variable from each of the six factors for use in predicting habitat suitability. Either approach may supplement and enhance the effectiveness of field surveys, especially in remote, rugged terrain and might be useful for inclusion into environmental impact sur-

veys in states where the Red-shouldered Hawk is classified as endangered or threatened.

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THE INFLUENCE OF WEATHER ON HAWK MOVEMENTS IN COASTAL NORTHERN CALIFORNIA

LINNEA S. HALL[1], ALLEN M. FISH[2], AND MICHAEL L. MORRISON[2]

ABSTRACT.—Sharp-shinned (*Accipiter striatus*), Cooper's (*A. cooperii*), and Red-tailed (*Buteo jamaicensis*) hawks, and the total species (19) occurring in the Marin Headlands, Marin County, California, were quantified in relation to seven weather variables. Peak counts of raptors occurred in mid- to late September, with counts largely composed of immature hawks. More adult hawks were counted in mid- to late October. Adult and immature Sharp-shinned and Cooper's hawk counts were correlated with days before and after cold fronts, increasing temperature, barometric pressure, wind speed, and decreasing fog cover. Numbers of adult and immature Red-tailed Hawks were correlated negatively with fog and days before cold fronts and positively with temperature and barometric pressure. Cold front presence or absence did not affect Red-tailed Hawk numbers in 1986–1988. Fewer accipiters and Red-tailed Hawks were counted with south winds (headwinds) blowing, and in 1988 more adult birds were counted with north winds (tailwinds). Increasing temperatures, decreasing fog, and an absence of headwinds were correlated the most with counts of all species in the Headlands; cold front presence or absence had no significant influence on numbers in 1986–1988. A decreasing number of days before and after cold fronts was also generally associated with counts. *Received 27 Sept. 1991, accepted 10 Feb. 1992.*

In 1985 the Golden Gate Raptor Observatory (GGRO) was established to monitor fall migration of diurnal raptors over the Marin Headlands, Marin County, California. Binford (1979) first documented large numbers of raptors moving through the headlands in 1972. Raptors heading south are "funneled" through the Marin peninsula by the Pacific Ocean on the west and the extensions of the San Francisco Bay on the east. Consequently, the birds can be counted each fall as they move to the tip of the peninsula and cross the bay. Here, we present the first analysis of weather and hawk data from the headlands site.

In the eastern United States, Europe, and the Middle East, there are many historic migration-viewing sites, from which most of the published literature on weather and hawk migration has come. Although some consistent relationships among weather factors and hawk counts have been found—such as those with wind direction and barometric pressure—much variation remains unexplained. Some variance probably stems from the problems inherent in single-site migration counts, i.e., a limited view of migratory movements (site bias) and a reliance on many different ob-

[1] Golden Gate Raptor Observatory, Building 201, Fort Mason, San Francisco, California 94123. (Present address LSH: School of Renewable Natural Resources, Univ. of Arizona, Tucson, Arizona 85721.)
[2] Dept. of Forestry and Resource Management, Univ. of California, Berkeley, California 94720.

servers (a count method bias) (see review in Kerlinger 1989:27,33). Thus, because a substantial proportion of birds is probably not counted (Alerstam 1978), any observed correlations apply only to those observed, and who were reacting to localized and ephemeral weather conditions. However, correlational analyses of local weather and flights are necessary, so that comparisons may be made among different sites and regions. Our objectives were to evaluate the influences of west coast weather on yearly hawk counts, and to compare the findings with those of other migration viewing sites. Because many migration researchers do not examine inter-year differences but instead look for synoptic patterns across multiple years, we assessed within- and between-year correlations of weather and hawk counts to see if there were any patterns. We assessed how 19 species moving through the headlands were affected by weather conditions, but concentrated on how counts of the most abundant migrating species (Cooper's [*Accipiter cooperi*], Sharp-shinned [*A. striatus*], and Red-Tailed [*Buteo jamaicensis*] hawks) were affected, with respect to age and yearly differences, and differential migration patterns.

METHODS

Data collection.—Raptors were counted daily from mid-August to mid-December 1986–1988. Counts were made from the top of Hill 129, a 275 m peak located at the southern tip of the Marin Headlands (37°50′long., 122°30′lat.) that afforded a 360° view of the sky. Volunteer observers (3–8, depending on the time of the season), trained to identify flying raptors, counted hawks each day of the season. At least one volunteer at the site each day was an experienced and adept observer. Observations were made from 09:00–16:00 h, except during days of heavy precipitation, dense fog, or high wind, when the view was obscured. Observers recorded and tracked the hawks as they flew south past Hill 129 and across the San Francisco Bay. Although a great number of birds were observed crossing, some of them undoubtedly doubled-back. This may have occurred especially during more inclement weather, when they might have been unwilling or unable to cross the Bay (Mueller and Berger 1967). In light of this, hawks were watched for as long as possible to reduce double-counting (Kerlinger 1989), but it is likely that a small (and unknown) percentage of our data reflects hawks counted twice.

Data were recorded on forms adapted from those of the Hawk Migration Association of North America (HMANA). Seven weather variables were chosen for the analyses, based on their associations with bird movements as observed in other studies (e.g., Haugh 1972, Able 1973, Alerstam 1978, Gauthreaux 1980, Titus et al. 1988): surface-level wind direction, wind speed, temperature, fog, barometric pressure, presence or absence of cold fronts, and number of days before and after frontal systems. Wind speeds were taken hourly on the edge of Hill 129 with a hand-held anemometer. Recordings of surface wind direction and temperature also were made hourly. The total number of minutes that observations took place each day was recorded. Fog cover was assessed by Hall from daily field notes that described the length of time Hill 129 and the Marin Headlands were covered. Daily barometric pressure (mm Hg) and presence or absence of frontal systems were obtained from National Oceanic and Atmospheric Administration daily weather maps (1986–1988; 04:00 PST) for the San Francisco Bay area and California. Cold fronts were recorded as "present"

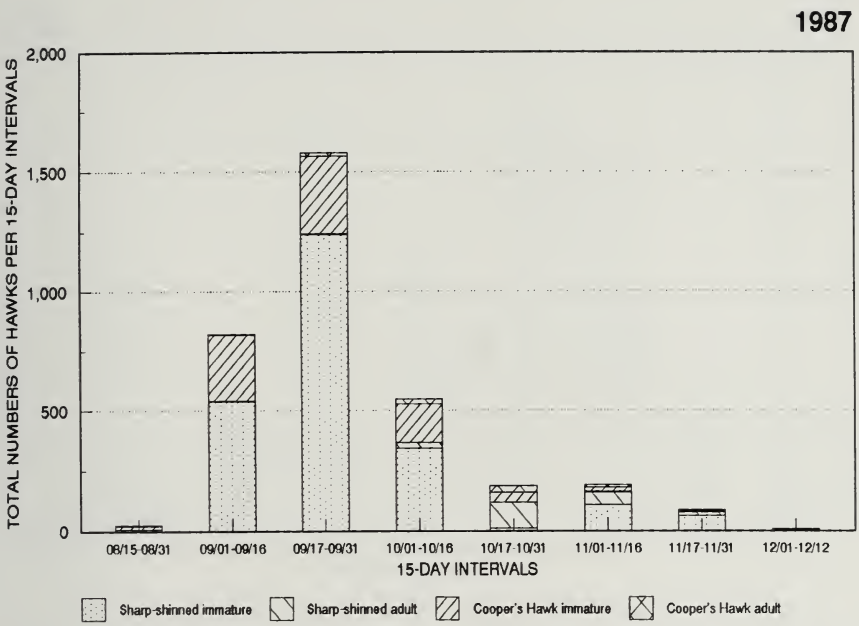

FIG. 1. Total numbers of Sharp-shinned and Cooper's hawks counted at the Marin Headlands, Marin Co., California, 1987, summarized by 15-day intervals.

if they were between 130° longitude and the coast of northern California on the sample day (since this noticeably affected weather conditions in the Headlands) or were determined to have come through the area during the past 24 h.

Analyses.—We analyzed 303 of 355 total sample days from 1986 to 1988. Days with <2 h of observations due to dense fog, rain, and no observations or available cold front information were removed. The resulting numbers of days sampled were: 1986, 98; 1987, 105; and 1988, 100. For 303 days the mean observation hours per day = 5.5 (SD = 1.13).

The numbers of observed hawks were summarized by 15-day intervals for each year, species, and age to provide descriptions of differential migration patterns (Figs. 1–5). As suggested by Richardson (1978), and used by researchers such as Titus and Mosher (1982) and Bednarz et al. (1990), we examined the annual distributions of hawk numbers to see what dates encompassed 95% of the observed migration. We then performed all subsequent analyses on these sample days (Table 1) to represent accurately each species' period of migration.

We analyzed the number of hawks per hour for each sample day for the 19 species counted in the Marin Headlands (total hawks) vs the seven weather variables. Species of hawks observed were: Turkey Vulture (*Cathartes aura*); Black-shouldered Kite (*Elanus caeruleus*); Northern Harrier (*Circus cyaneus*); Sharp-shinned Hawk; Cooper's Hawk; Northern Goshawks (*Accipiter gentilis*); Red-tailed Hawk; Red-shouldered Hawk (*Buteo lineatus*); Swainson's Hawk (*B. swainsoni*); Broad-winged Hawk (*B. platypterus*); Rough-legged Hawk (*B. lagopus*); Ferruginous Hawk (*B. regalis*); Golden Eagle (*Aquila chrysaetos*); Bald Eagle (*Haliaeetus leucocephalus*); Prairie Falcon (*Falco mexicanus*); Peregrine Falcon (*F. peregrinus*); Merlin (*F. columbarius*); American Kestrel (*F. sparverius*); and Osprey (*Pandion haliaetus*).

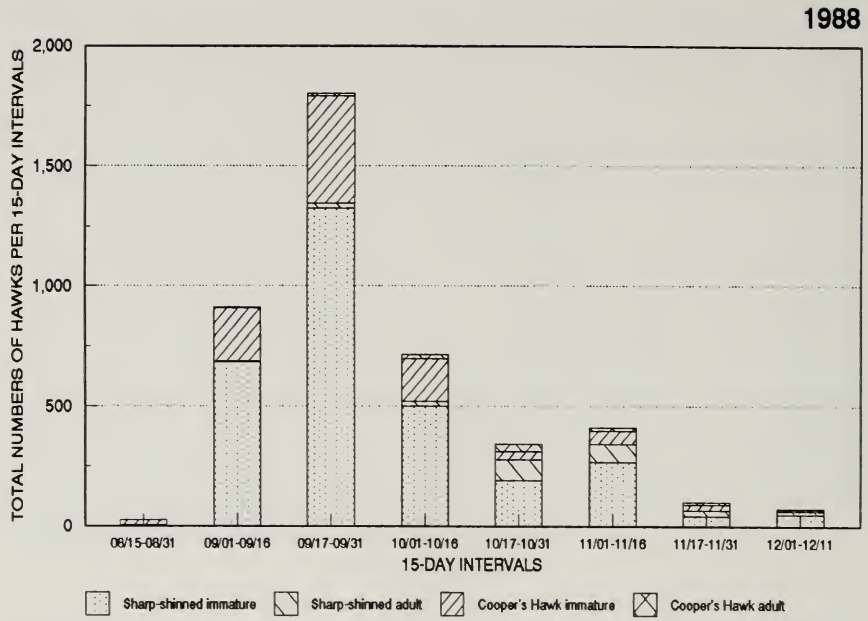

FIG. 2. Total numbers of Sharp-shinned and Cooper's hawks counted at the Marin Headlands, Marin Co., California, 1988, summarized by 15-day intervals.

Numbers of Sharp-shinned, Cooper's, and Red-tailed hawks were also analyzed in relation to the seven weather variables for 1986–1988 and for each year independently. In 1986, Sharp-shinned and Cooper's hawks were counted but not aged, and so we did not conduct analyses on the immature or adult age groups; however, the numbers were included in the total hawk analyses for 1986.

We conducted a Kolmogorov-Smirnoff goodness-of-fit test (two-tailed; Zar 1984:55–58) to see if hawk numbers were normally distributed. Of all the hawk categories, only adult Red-tailed ($P = 0.10$) and immature Sharp-shinned hawk numbers ($P = 0.07$) in 1988 were distributed normally. Therefore, we used Spearman's rank correlations (Zar 1984:318–320) to determine associations of wind directions and cold fronts with hawk numbers. Daily surface wind directions were summarized from hourly recordings, giving a predominant or shifting wind direction for each sample day. The resulting wind directions were combined into six final categories: the four cardinal directions, a no wind category, and a variable winds category (indicating direction shifts during the day). Kruskal-Wallis analysis of variance (K-W ANOVA; Zar 1984:250, and see Haugh 1972 for similar data treatment) was conducted for the three species and for total hawks versus the wind categories. Fog coverage was recorded daily, and for the analyses was converted to codes: 0 = no fog; 1 = up to, but no more than one-half day of fog coverage; and 2 = more than one-half day, but no more than three-quarters of the day under fog. The frequencies of coverage were determined and tested for differences among years (χ^2 analysis with Cramer's phi coefficient [Zar 1984:322]), and the variable was entered into the correlation analysis. Cold fronts were analyzed by Kruskal-Wallis analysis of variance for the number of hawks observed per hour versus the

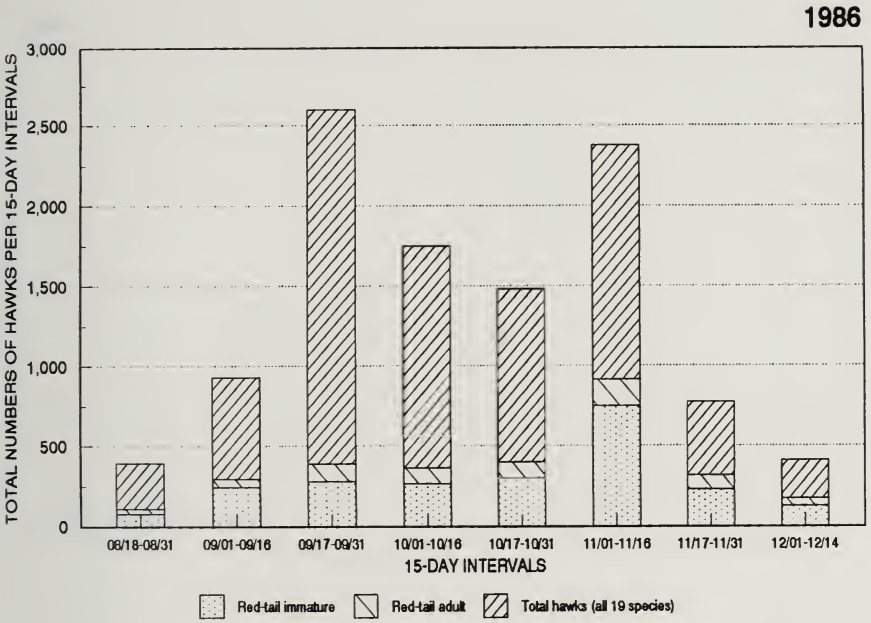

FIG. 3. Total numbers of Red-tailed Hawks and all 19 species of hawks counted at the Marin Headlands, Marin Co., California, 1986, summarized by 15-day intervals.

presence or absence of a cold front. Number of days before and number of days after cold fronts were also included in the Spearman correlation analysis.

We used SPSS-X (SPSS 1988) for all statistical analyses. Barometric pressure, temperature, and wind speed were included in the correlation analysis to see if multicollinearity was high among weather variables (Morrison et al. 1992). Seasonal averages of numbers of hawks, temperatures, barometric pressures, and wind speeds were tested for differences among years by a Kruskal-Wallis ANOVA. All values reported in the text are significant at $P < 0.05$ unless otherwise noted.

RESULTS

Average seasonal temperatures and surface wind speeds differed significantly among years (Table 2), as did percent frequencies of fog cover (Table 3). The 1987 season was the warmest overall and also had the most number of days with westerly winds blowing; the 1986 season had the lowest average wind speeds. North and west winds predominated in the headlands, however, in all three years, variable winds also accounted for a similar proportion of the totals (Table 3). Overall, temperature was negatively correlated with wind speed and fog (i.e., as temperature increased the latter two decreased; $r_s = -0.25$ and -0.30, respectively). Temperature was positively correlated with days before and after cold

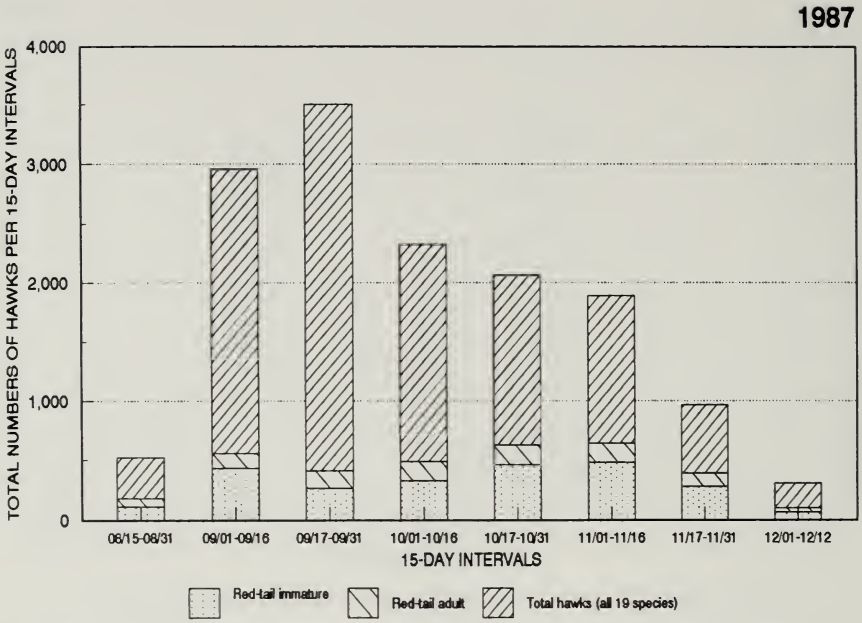

FIG. 4. Total numbers of Red-tailed Hawks and all 19 species of hawks counted at the Marin Headlands, Marin Co., California, 1987, summarized by 15-day intervals.

fronts (indicating that days farther from frontal systems were the warmest; $r_s = 0.23$ and 0.27). Barometric pressure was negatively correlated with fog, wind speed, and days before and after cold fronts ($r_s = -0.12$ to -0.28). Fog was positively associated with days before cold fronts ($r_s = 0.17$). Fronts passed near or through the Marin Headlands on 48 of 303 sample days (Table 3). Days before and after cold fronts were correlated with each other ($r_s = 0.51$).

Total numbers of hawks counted 1986–1988 are summarized in Table 1 for those dates encompassing 95% of the migration seasons in each year. From 1986 to 1988 there were 3490 total Cooper's Hawks counted (aged and unknown-aged hawks combined); 9003 Sharp-shinned Hawks; 10,424 Red-tailed Hawks; and 35,921 hawks of all 19 species together.

Average seasonal numbers of adult Sharp-shinned Hawks per hour were not significantly different between 1987 and 1988. There were no significant differences in mean numbers of adult or immature Cooper's Hawks between 1987 and 1988, or in the numbers of Red-tailed Hawks, for both ages, in 1986–1988. The number of hawks did vary between 1986 and 1988 ($P = 0.03$; Table 4). All species were correlated with each other during the three years (P's < 0.001; r_s's = 0.25–0.98).

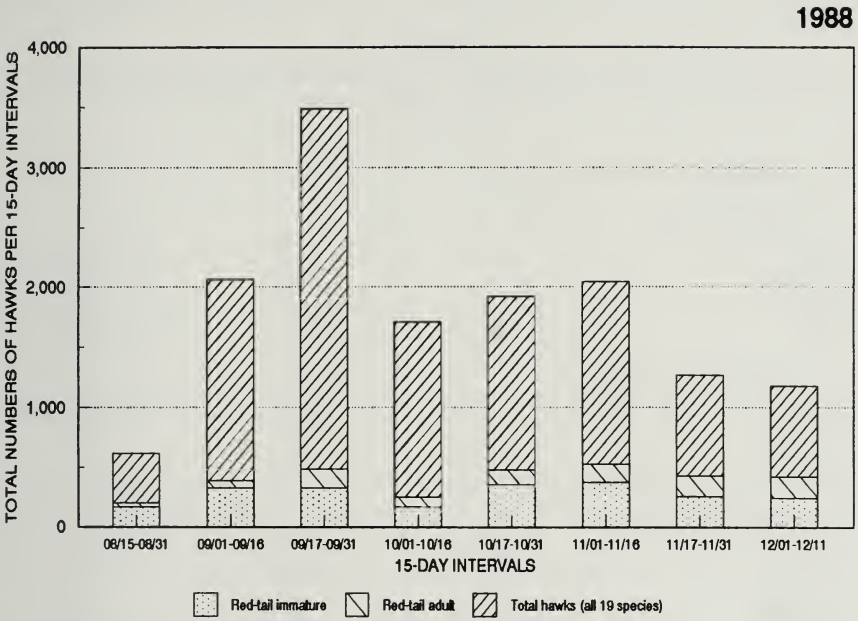

FIG. 5. Total numbers of Red-tailed Hawks and all 19 species of hawks counted at the Marin Headlands, Marin Co., California, 1988, summarized by 15-day intervals.

Peaks in counts of immature Cooper's and Sharp-shinned hawks occurred in mid-September in 1987 and 1988 (Figs. 1 and 2, respectively); adult accipiters were counted mostly in mid-October. Peaks in immature Red-tailed Hawk counts occurred in September and early November 1986–1988; the largest peak in numbers occurred in early November 1986 (Figs. 3–5). Adult Red-tailed Hawks were counted fairly consistently across the seasons, although in early November 1986 there was a small peak in numbers (Figs. 3–5). For all hawk species together, peak counts were in mid- to late September; however, in 1986 there was a second peak in numbers in early November (Figs. 3–5).

Sharp-shinned Hawks.—In 1987, no Spearman rank correlations for adults were significant, but sightings of adults were associated with decreasing fog and wind speed, increasing temperature and pressure, and days before and after fronts (Table 5). In 1988 adults were positively correlated with days after fronts, and in the Kruskal-Wallis ANOVA, tended to be associated with an absence of cold fronts ($P = 0.08$). In 1987, immature birds were negatively correlated with days before and after cold fronts, and they were consistently associated with increasing temperatures and wind speeds (Table 5). They were also observed more on days without

TABLE 1

TOTAL NUMBERS OF HAWKS COUNTED AT THE MARIN HEADLANDS, MARIN COUNTY, CALIFORNIA, IN 1986–1988

Species Age class	Year		
	1986[a]	1987	1988
Cooper's Hawk			
Adult	—	88	86
Immature	—	837	972
Unknown	904	427	176
Total	904[b]	1352	1234
Sharp-shinned Hawk			
Adult	—	201	242
Immature	—	2306	3057
Unknown	1622	1007	568
Total	1622	3514	3867
Red-tailed Hawk			
Adult	682	938	961
Immature	2238	2309	2207
Unknown	219	543	327
Total	3139	3790	3495
Total hawks (all ages)			
Total	7671	10,918	17,332

[a] Dates used for total numbers represent 95% of all species' migration seasons in each year: 1986, 20 Aug.–14 Dec.; 1987, 20 Aug.–12 Dec.; 1988, 20 Aug.–11 Dec.

[b] Numbers are total numbers of accipiters (adults and immatures together) for 1986, since these hawks were not identified as to age in that year.

cold fronts ($P = 0.02$, K-W ANOVA), and fewer birds were counted when south winds (headwinds) were blowing ($P = 0.04$; Table 6).

Cooper's Hawks.—In 1987, adult accipiter numbers were correlated with a greater number of days before cold fronts (Table 5). They were not counted as much when fronts were present (K-W ANOVA, $P = 0.04$). In 1988, there were no significant correlations, but for both years the counts were associated with decreasing fog, increasing temperatures, and a greater number of days after cold fronts. In 1987 and 1988, immatures were negatively associated with days after cold fronts; in 1987, days before fronts were also negatively correlated with number of immatures (Table 5). Temperature was positively associated with observations of immatures in 1988, and there also was a trend toward counting more immatures with increasing pressure, decreasing fog, and increasing wind speed. In 1987, there tended to be fewer young birds counted with south winds in the Marin Headlands ($P = 0.07$; Table 6); this pattern was significant in 1988 ($P < 0.01$).

TABLE 2

MEAN SEASONAL TEMPERATURES, BAROMETRIC PRESSURES, AND SURFACE WIND SPEEDS AT THE MARIN HEADLANDS, MARIN COUNTY, CALIFORNIA, FROM AUGUST TO DECEMBER, 1986–1988

Variables	1986 $\bar{x}$ N = 98 days	SD	1987 $\bar{x}$ N = 105	SD	1988 $\bar{x}$ N = 100	SD
Temperature (°C)	16.4 A[a]	3.52	17.3 AB	3.92	15.9 AC	4.27
Barometric pressure (mmHg)	1017.2 A	3.97	1017.3 A	3.25	1016.9 A	4.93
Surface wind speed ($km\text{-}h^{-1}$)	4.0 A	2.50	7.2 B	3.50	7.7 B	3.20

[a] Values with different letters are significantly different among years ($P \leq 0.05$); Kruskal-Wallis analysis of variance.

Red-tailed Hawks.—In 1986–1988, fog and days before cold fronts were consistently negatively correlated with adult hawks, and temperature and pressure were correlated positively with adult hawk counts (Table 5). There were no effects of cold front presence or absence on adult hawk numbers in 1986–1988 (K-W ANOVA, all P's > 0.4). Wind direction was significant only in 1988, when more birds were counted on days with

TABLE 3

PERCENT FREQUENCIES OF FOG, COLD FRONTS, AND SURFACE WIND DIRECTIONS AT THE MARIN HEADLANDS

Variable	Frequency 1986 N = 98 days	1987 N = 105	1988 N = 100
Fog[a]			
0	65	71	68
1	16	11	14
2	15	17	18
Front			
Absent	81	84	86
Present	18	15	14
Surface wind direction			
North	38	22	26
South	7	8	12
East	5	2	0
West	27	37	35
No wind	1	2	0
Variable	21	28	27

[a] See text for explanation.

TABLE 4

MEAN NUMBER OF HAWKS·H^{-1}·DAY^{-1} OBSERVED AT THE MARIN HEADLANDS

Species	1986 $\bar{x}$ N = 98 days	1986 SD N = 98 days	1987 $\bar{x}$ N = 105	1987 SD N = 105	1988 $\bar{x}$ N = 100	1988 SD N = 100
Sharp-shinned Hawk						
Immature	—[a]		3.6	7.17	5.1	7.51
Adult	—		0.3	0.47	0.4	0.72
Cooper's Hawk						
Immature	—		1.3	2.26	1.7	2.62
Adult	—		0.1	2.81	0.2	0.33
Red-tailed Hawk						
Immature	4.1	3.93	3.7	3.46	3.9	3.73
Adult	1.3	1.21	1.5	1.36	1.7	1.53
Total Hawks	13.8	11.92 A	17.3	16.68 AB[b]	19.6	15.81 B

[a] Accipiters were not aged in 1986 and were not included in the analysis.
[b] Values with different letters are significantly different at $P \leq 0.05$, Kruskal-Wallis analysis of variance.

north winds (Table 6). Fog, temperature, and days before cold fronts were significantly correlated with the numbers of immature birds in 1986–1988, and the birds were also consistently associated with rising pressure and fewer days after a front (Table 5). In the Kruskal-Wallis ANOVA, immature Red-tailed Hawks were not associated with the presence or absence of cold fronts (all P's > 0.5). In 1987, there tended to be fewer immatures counted with south winds and more with east winds ($P = 0.08$), and this pattern was significant in 1986 ($P = 0.03$) and 1988 ($P = 0.01$) (Table 6).

Total hawks.—Overall, temperature and fog were most highly correlated with the counts of all species in the Marin Headlands (e.g., highest r's = 0.45 [temperature] and −0.30 [fog]). However, there were also consistent negative correlations with the number of days before a cold front (i.e., more hawks counted closer to a frontal passage). Cold front presence or absence had no significant influences on the total numbers counted in 1986–1988 (all P's > 0.5). Fewer hawks were counted with south and no winds in 1986 ($P = 0.05$) and 1988 ($P = 0.04$) (Table 6).

DISCUSSION

Increasing temperatures and decreasing fog influenced the numbers of hawks counted in the Marin Headlands, although the resulting correlations were weak (i.e., no $r_s > 0.51$). Of the 102 correlations of hawk numbers versus weather variables, only 26 were significant. This equates to 28%,

TABLE 5

SIGNIFICANT SPEARMAN RANK CORRELATION COEFFICIENTS, AND NONSIGNIFICANT SIGNS FOR COOPER'S, SHARP-SHINNED, RED-TAILED, AND TOTAL HAWK NUMBERS VS SIX WEATHER VARIABLES

Species		Correlation coefficient (r_s)					
Age	Year	B[b]	F	T	WS	DBF	DAF
Sharp-shinned Hawk							
Adult	1987	+[c]	−	+	−	+	+
	1988	+	−	+	−	+	+0.32[d]
Immature	1987	−	+	+	+	−0.28	−0.43
	1988	−	−	+0.51	+	+	−
Cooper's Hawk							
Adult	1987	−	−	+	+	+0.29	+
	1988	+	−	+	−	−	+
Immature	1987	+	−	+	+	−0.28	−0.42
	1988	+	−	+0.49	+	+	−0.28
Red-tailed Hawk							
Adult	1986	+	−0.30	+	+	−	+
	1987	+	−0.30	+0.22	+	−	−
	1988	+0.48	−0.50	+	−	−0.24	−
Immature	1986	+	−0.22	+0.23	+	−0.25	−
	1987	+	−0.40	+0.27	−	−	−
	1988	+	−0.34	+0.32	−	−0.24	−
Total hawks (all species counted)							
	1986	−	−0.30	+0.35	−	−	+
	1987	−	−0.30	+0.41	+	−	−
	1988	+	−0.29	+0.45	−	−	−

[a] Accipiters were not aged in 1986 and were not included in the analyses.
[b] Variable notation: B = barometric pressure; F = fog; T = temperature; WS = wind speed; DBF = number of days before cold fronts; DAF = number of days after cold fronts.
[c] "+" = positive but nonsignificant correlation; "−" = negative nonsignificant correlation.
[d] All values are significant at $P < 0.05$.

which is not significantly different from what would be expected by random chance (Rohlf and Sokal 1981:156–159). However, the consistent associations with temperature and fog, as well as with wind direction, indicated that these variables did have impact on our counts.

A decreasing number of days before cold fronts was associated with changes in the magnitudes of the Red-tailed and total hawks counted, thus indicating that more birds may have been counted closer to the days that cold fronts passed along the northwest coast. There were notable inter- and intraspecific differences: only counts of Red-tailed Hawks were affected by fog, and more adult Cooper's and Sharp-shinned hawks were

TABLE 6

MEAN RANKS AND *P*-VALUES FROM A TWO-TAILED KRUSKAL-WALLIS ANALYSIS OF VARIANCE OF HAWKS·H^{-1}·DAY^{-1} VS WIND DIRECTION[a]

Species			Mean rank					
Age	Year	*P*	North	South	East	West	No wind	Variable wind
Cooper's Hawks								
Adults	1987	0.61	51.8	53.7	72.7	50.0	58.8	46.1
	1988	0.17	48.3	52.2	—[b]	41.6	—	55.8
Immatures	1987	0.07	49.4	28.5	58.3	59.4	39.5	46.6
	1988	0.00	39.5	27.4	—	59.1	—	53.4
Sharp-shinned Hawks								
Adults	1987	0.46	52.9	47.6	65.0	44.0	56.8	56.3
	1988	0.32	55.7	50.6	—	42.6	—	48.1
Immatures	1987	0.14	50.5	26.9	72.3	53.9	45.5	51.6
	1988	0.04	42.0	33.8	—	57.1	—	50.7
Red-tailed Hawks								
Adults	1986	0.37	52.1	36.6	58.2	44.2	8.0	49.3
	1987	0.61	55.6	40.2	72.3	49.4	50.5	49.1
	1988	0.00	66.3	44.3	—	38.2	—	46.4
Immatures	1986	0.03	54.8	25.5	66.4	40.3	24.0	50.8
	1987	0.08	52.0	24.8	72.3	49.7	51.3	56.3
	1988	0.01	56.7	25.0	—	48.4	—	51.5
Total hawks (all species counted)								
	1986	0.05	55.6	32.6	52.0	38.1	11.5	54.1
	1987	0.26	52.1	28.4	66.3	52.8	45.5	52.1
	1988	0.04	49.9	27.4	—	51.3	—	53.4

[a] Accipiters were not aged in 1986 and were not included in the analysis.
[b] During the 1988 season, there were no sample days recorded with east or no winds blowing.

seen on days farther away from cold fronts. Differences in results between hawk ages versus cold front and barometric pressure variables could have been caused by having much smaller sample sizes for adult Cooper's and Sharp-shinned hawks than for immatures.

Our results were comparable to the findings of other researchers. Titus and Mosher (1982), for example, found that increased migration of Sharp-shinned, Red-tailed, and Broad-winged (*B. platypterus*) hawks was correlated with warm temperatures in the eastern United States. Similarly, Millsap and Zook (1988) reported that movements of raptors in Nevada occurred during fair weather in autumn. Studies in other areas of the United States and coastal Europe have demonstrated, however, that large fall movements of birds and raptors primarily are related to low or falling

temperatures and rising pressure (e.g., Haugh 1972, Alerstam 1978). This type of weather is excellent for soaring raptors, and commonly occurs after the passage of the cold fronts (Able 1973, Gauthreaux 1980:154, Millsap and Zook 1988), with accompanying favorable winds and rising pressure (Haugh 1972). It is likely that the west coast, in general, experiences warmer temperatures than does the east coast after frontal movements in the fall, leading to the relatively high correlations of hawks with increasing temperatures and pressure.

The influences of cold fronts on hawk migration have been discussed by many researchers (e.g., Mueller and Berger 1961, Heintzelman 1975, Alerstam 1981). Numbers of migrants counted in the east have been seen to increase dramatically after the passage of a front (see Haugh 1972 for review; Able 1973), when inclement weather conditions have subsided. Our data showed that, generally, more hawks were counted closer to the passage of a front, either in the days before or the days after, although adult accipiters seemed to be counted more as the number of days after fronts increased. Increased magnitudes of flight around fronts could have been due to the instability of these low-pressure areas, because the up- and downdraft wind conditions caused by the fronts may have been good for soaring and gliding (Haugh 1972). However, increased counts for some of the birds could also have resulted from the hawks being forced to stopover in the Marin Headlands while the front passed and then to move on in a "wave" after the storm.

Fog strongly influenced Red-tailed Hawk counts. Several explanations for the decreased numbers we saw can be given. First, we may have missed counting a significant proportion of the birds because of reduced visibility. Or, the fog may have deterred migration because of a lack of visual topographical cues (as Binford noted occurring with hawks in the Marin Headlands in 1970–1977 [Macrae 1985]). Or finally, the fog may have made the hawks more sensitive to flying near water, because some land birds are averse to flying over large bodies of water in ephemeral weather conditions (Mueller and Berger 1967; review in Kerlinger 1989). Haugh (1972) likewise found a greater tendency with Red-tailed Hawks in the eastern United States to interrupt their migration when weather conditions deteriorated and to resume flight when conditions again became "stimulatory."

Researchers have intensively studied the relation of wind direction and wind speed to flight (e.g., Evans and Lathbury 1973, Able 1973, Gauthreaux 1980), and the general consensus is that birds migrating south fly significantly more with tailwinds (usually north or northwest winds) than with headwinds (usually south or southeast winds). Our findings for hawks in the Marin Headlands also showed that there were fewer hawks counted

when south winds were predominant, and adult Red-tailed Hawks were observed more with north winds. Up to a certain level, increasing wind speed may also facilitate migration (because updrafts are produced, allowing more gliding flight), but beyond this, migration may be impeded (e.g., Alerstam 1978). For the most part, immature accipiters and adult Red-tails were associated with increased surface-level winds at the Marin Headlands, whereas the other hawks reacted variably to wind speeds. Large hawks (with greater wing length : wing breadth ratios) may need faster wind speeds because they need more lift to migrate more efficiently (Pettingill 1970:24). However, our results were too inconclusive to further address this point.

This study has shown that the numbers of hawks counted in the Marin Headlands were influenced by localized, west coast weather patterns. However, the weak correlations also indicated that local weather accounted for only a small portion of the observed variability in the counts. Other factors such as *Zugdisposition* (physiological readiness) and *Zugunruhe* (migratory activity) play significant parts in determining hawk movements in fall, and a factor such as day of the season may also be an important determinant of species' migration, irrespective of weather conditions. Finally, fall migration counts may be especially dependent on the conditions (e.g., weather, foraging) located to the north of the migration study site at a given time, because the local northern situation affects the number of birds migrating south past the study site. However, hawks migrating in fall along the west coast of North America are obviously influenced by the same weather variables that affect birds in eastern North America and Europe, with one difference appearing to be that hawks in the Marin Headlands are counted more when they have warm temperatures and no fog obscuring the San Francisco Bay. These conditions may act to disperse hawks from migration-viewing sites, leading to decreased counts.

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DAILY AND SEASONAL ACTIVITY PATTERNS OF COMMON RAVENS IN SOUTHWESTERN IDAHO

KATHLEEN A. ENGEL[1] AND LEONARD S. YOUNG[2]

ABSTRACT.—From May 1985 through February 1987, we recorded the diurnal activity budgets of 26 radio-marked Common Ravens (*Corvus corax*) in southwestern Idaho. Resting (63% of observations) was the predominant diurnal activity, followed by feeding (13%), flying (13%), and moving along the ground (11%). Raven activity budgets differed significantly among seasons, times of day, and habitat types but not among age classes. Although seasonal times spent in locomotory activities were similar, during spring the proportion of time spent feeding nearly tripled and resting decreased. Ravens exhibited no distinct hourly pattern in feeding during winter; however, ravens fed primarily in the morning during spring and crepuscularly during summer and fall. Ravens mainly fed while in agricultural land and rested while in shrub- or grass-dominated rangeland. Our data suggest that seasonal activity budgets of ravens in southwestern Idaho are influenced by characteristics of the food supply and preparation for reproduction, and that daily patterns of activity are influenced by ambient temperature and food availability. *Received 8 May 1991, accepted 15 Jan. 1992.*

Verner (1965) suggested that every species has an optimal activity budget specifically adapted to local environmental conditions. The ability to vary time and energy budgets is a "potent means of coping with a changing environment and retaining some degree of adaptation to it" (Pianka 1974). Reproductive activities (Verner 1965), food availability (Boxall and Lein 1989), ambient temperature (Verbeek 1964, 1972), day length (Gibb 1956), and habitat (Eberhardt et al. 1989) can vary temporally, and all have been found to influence avian activity budgets. The degree to which activity budgets are influenced by daily and seasonal changes in the environment can provide important insight into the mechanisms by which an animal adapts to its environment.

The Common Raven (*Corvus corax*) is non-migratory and occurs across a wide variety of habitats throughout the northern hemisphere, ranging from the high Arctic tundra to the desert communities of Mexico (Goodwin 1976). Little is known about how ravens cope with such environmental extremes (Schwan and Williams 1978). Although basic to understanding the ecology of an animal, the activity budget of Common Ravens has not been described. We report the daily and seasonal diurnal activity budgets of Common Ravens in southwestern Idaho and examine

[1] Environmental Services Dept., Pacific Power, 920 S.W. Sixth Ave., 800 PFFC, Portland, Oregon 97204. (Present address KAE: Dept. of Wildlife Ecology, Univ. of Wisconsin, 226 Russell Laboratories, Madison, Wisconsin 53706.)

[2] Snake River Birds of Prey Research Project, Bureau of Land Management, 3948 Development Ave., Boise, Idaho 83705. (Present address LSY: Washington Dept. of Natural Resources, Forest Land Management Div., MQ-11, Olympia, Washington 98504.)

the effects of time of year, time of day, ambient temperature, day length, age, and habitat on raven activity budgets. Assuming the most important activity of an animal is to obtain sufficient energy to exist, we focus particularly on the amount of time devoted to feeding.

STUDY AREA AND METHODS

We observed ravens from communal roosts located on towers of a 500-kV transmission line in southwestern Idaho (Engel et al. 1992). Livestock-grazed shrub-steppe vegetation (West 1983) and agriculture dominate this area. Major vegetation includes big sagebrush (*Artemesia tridentata*), grasses (*Poa* and *Bromus* spp.), black greasewood (*Sarcobatus vermiculatus*), and shadscale (*Atriplex confertifolia*). A more detailed description of the vegetation and topography can be found in a U.S. Department of the Interior report (1979). From 1978–1987, mean annual temperature averaged 10.1 ± 1.1°C, and annual precipitation averaged 36.4 cm ± 7.8 cm (U.S. Department of Commerce, unpubl. data). Each year, about two-thirds of the annual precipitation fell from October to March.

We used padded leghold traps and a rocket net to capture ravens (Engel and Young 1989a). Ages of captured ravens were determined by palate color and classified as juveniles (<1 year old), subadults (≥1 year old and <3 years old), or adults (≥3 years old; Kerttu 1973). Juvenile ravens were also captured by hand as fledglings (35–40 days old) at nest sites in the vicinity of communal roosts. Captured ravens were fitted with a back-mounted radio transmitter weighing either ca 21 g (ravens ≤950 g) or ca 30–32 g (ravens >950 g), an aluminum U.S. Fish and Wildlife Service leg band, and a yellow, vinyl-coated nylon, piercing patagial marker on each wing. Patagial markers were numbered uniquely to facilitate identification of individual birds in the field.

From May 1985 through February 1987, we followed radio-marked ravens during four randomly selected observation days each week. One raven was followed on each observation day, from the time the raven left its roost in the morning (ca 30 min before sunrise) until it returned to its roost in the evening (ca 30 min after sunset). Ravens to be tracked were selected sequentially from the sample pool of radio-marked birds and were not tracked more than once per week even if fewer than four birds were available for tracking. Ravens were included in the sample pool until they either died, left the study area, or their transmitters expired.

Ravens were observed from vehicles equipped with 15–60× spotting scopes and 7- to 10-power binoculars. We generally approached no closer than 400 m from the focal raven to avoid influencing its behavior. While the focal raven was in view, we recorded its activity every five min. Activities were classified as either feeding, flying, resting (sleeping, perching, standing, or preening), or moving (traveling along the ground). Maintenance activities, such as preening, occurred infrequently, thus we combined them with "resting" activities. Ravens were considered to be feeding if they were observed either swallowing or inserting their bills into the soil or a food item. In addition, habitat type was recorded for all non-flying observations and was classified as either shrub (i.e., shrub-dominated rangeland), grass (i.e., grass-dominated rangeland), pasture, mowed or stubble agricultural field, riparian, or other habitat. Pasture was distinguished from grass-dominated rangeland in that pasture was irrigated, and rangeland was not. Nine additional habitat categories were recorded initially, but each occurred so infrequently that we combined them into "other" habitat for analysis.

Ravens were considered the sample units for statistical analysis. The proportion of time spent engaged in each activity was summarized for individual ravens in each statistical subgroup and expressed as the number of observations in an activity category divided by the total number of observations for that bird. Proportions were arcsine transformed before

TABLE 1

PERCENTAGES OF MONTHLY OBSERVATIONS DURING WHICH COMMON RAVENS ENGAGED IN VARIOUS ACTIVITIES IN SOUTHWESTERN IDAHO, MAY 1985–FEBRUARY 1987

Month	Feeding (SD)[a]	Flying (SD)	Resting (SD)	Moving (SD)	N
Jan.	16.9 (9.3)	9.1 (4.5)	52.8 (10.2)	21.1 (8.5)	5
Feb.	23.2 (22.0)	9.5 (5.7)	52.9 (20.2)	14.4 (12.0)	6
Mar.	39.6 (9.6)	14.6 (15.0)	34.5 (12.9)	11.3 (8.9)	3
Apr.	61.3 (54.7)	8.1 (11.4)	24.2 (34.2)	6.5 (9.1)	2
May	10.1 (9.8)	19.5 (12.6)	63.7 (17.7)	6.8 (8.1)	8
June	14.2 (5.4)	15.0 (7.1)	63.6 (10.9)	7.2 (5.6)	6
July	11.2 (7.1)	9.1 (6.8)	70.2 (12.8)	9.4 (8.0)	14
Aug.	10.5 (5.2)	9.6 (4.2)	68.0 (16.2)	11.9 (10.7)	11
Sept.	5.1 (7.0)	7.6 (5.5)	79.6 (17.2)	7.7 (8.3)	7
Oct.	10.7 (9.2)	10.7 (8.0)	69.1 (15.5)	9.4 (11.5)	6
Nov.	11.0 (9.0)	13.8 (5.6)	58.6 (15.5)	16.7 (15.3)	5
Dec.	14.1 (6.9)	14.4 (10.1)	55.3 (15.6)	16.2 (18.0)	6

[a] SD = standard deviation.

analysis (Zar 1974). Observations were grouped into four seasons: spring (February–April), summer (May–July), fall (August–October), and winter (November–January). Boundaries for these seasonal breaks were determined by gross changes in weather and raven diet (Engel and Young 1989b).

We used two-way analysis of variance (ANOVA) tests to examine seasonal differences in the proportion of the daytime spent engaged in each activity between years, among age classes, and among habitat types. If a significant difference was found with no significant interaction between treatments, one-way ANOVA was used to test for differences in the proportions of time devoted to each activity among seasons, ages, and/or habitat types, respectively. If significant differences were found, then Tukey's Honestly Significant Difference test (Tukey HSD) was used to locate between which seasons, age classes, or habitats differences existed. Analysis of covariance (ANCOVA) was used to test for a linear hourly trend (e.g., increase or decrease) in the proportion of time spent engaged in each activity and to test for seasonal differences in the hourly trend if it existed.

Due to continual addition and loss of marked ravens to and from the sample pool, sampling was not distributed evenly among all statistical subgroups. Thus, age-by-season comparisons could be made only for summer and fall when all three age classes were represented. All statistical tests were evaluated at the $P < 0.05$ level of significance.

RESULTS

We obtained 7753 5-min activity observations from 26 radio-marked ravens—14 adults, five subadults, and seven juveniles. Resting ($\bar{x} = 63\% \pm 14\%$ of observations) was by far the predominant diurnal activity of ravens, followed by feeding ($\bar{x} = 13\% \pm 10\%$), flying ($\bar{x} = 13\% \pm 9\%$), and moving ($\bar{x} = 11\% \pm 7\%$).

Seasonal activity budget.—The proportions of diurnal time spent flying and moving were similar throughout the year (one-way ANOVA, *P*s >

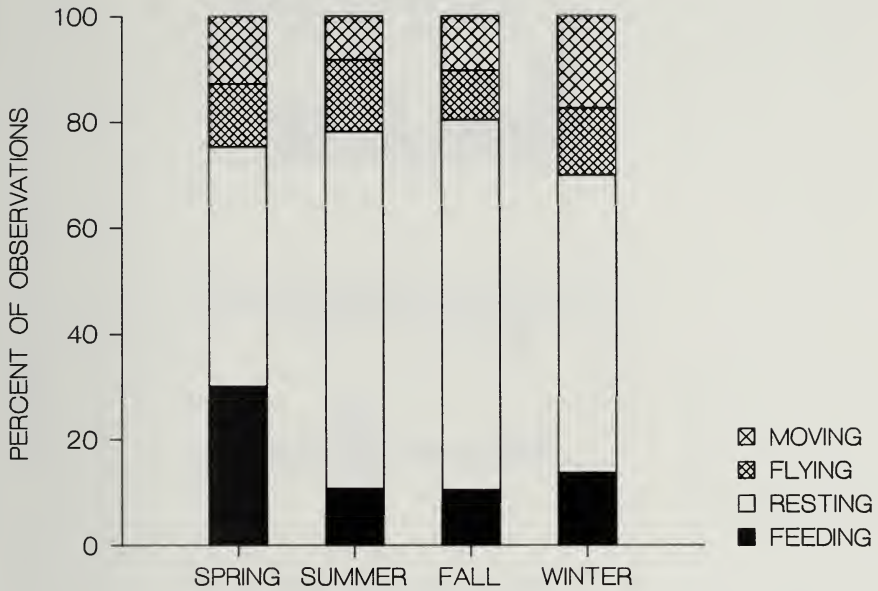

FIG. 1. Percentages of seasonal observations during which Common Ravens engaged in various activities, May 1985–February 1987.

0.30); in any given season, individual ravens spent 9–14% of the day flying and 8–18% of the day moving (Table 1; Fig. 1). The proportions of time ravens devoted to feeding and resting, however, differed significantly among seasons (one-way ANOVA, Ps < 0.01). Ravens spent similar proportions of time feeding from summer through winter (Tukey HSD, Ps > 0.79) but spent nearly three times as much time feeding during spring (Tukey HSD, Ps < 0.02). In addition, ravens spent more time resting during summer and fall than during spring (Tukey HSD, Ps < 0.05). Except for the proportion of time spent moving (two-way ANOVA, $P < 0.01$), these seasonal relationships were consistent between years (two-way ANOVA, Ps > 0.15).

We found no significant difference in the proportions of time ravens devoted to various activities among age classes (summer and fall only; two-way ANOVA, Ps > 0.14); this lack of difference was consistent between summer and fall (two-way ANOVA, Ps > 0.31).

Daily activity budget.—Hourly patterns in both the percentages of time spent feeding and flying differed significantly among seasons (ANCOVA, Ps < 0.04; Fig. 2). During spring, the proportion of each hour devoted to feeding decreased throughout the day, while during summer and fall, feeding maxima appeared bimodally distributed. No distinct hourly pat-

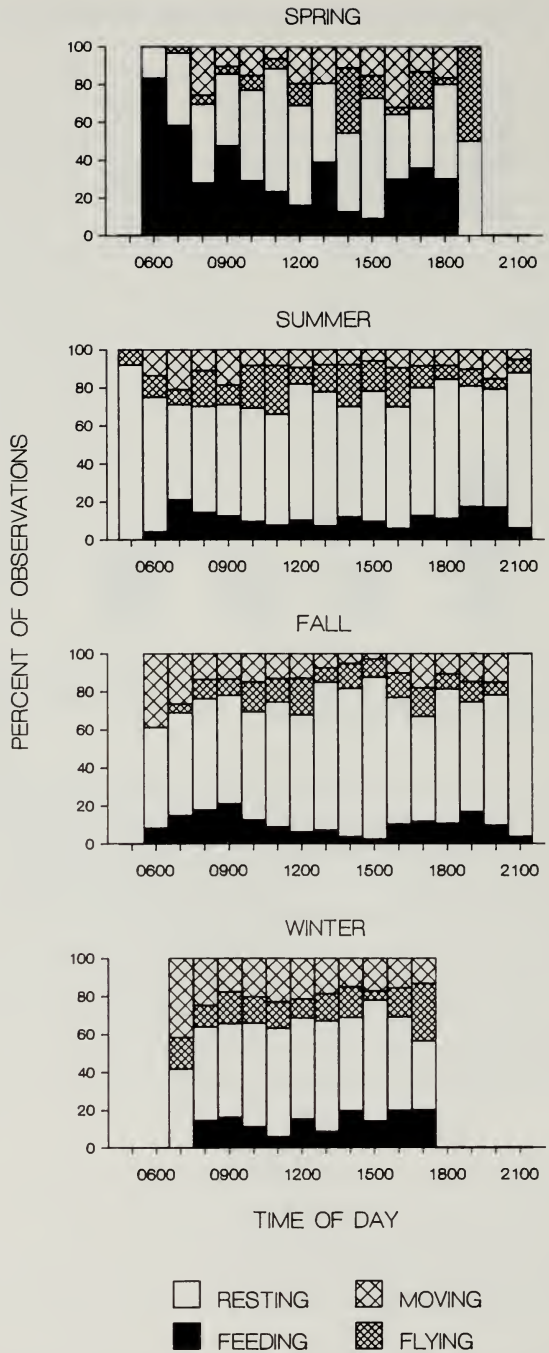

FIG. 2. Percentages of observations during which Common Ravens engaged in various activities in different seasons and times of day, May 1985–February 1987.

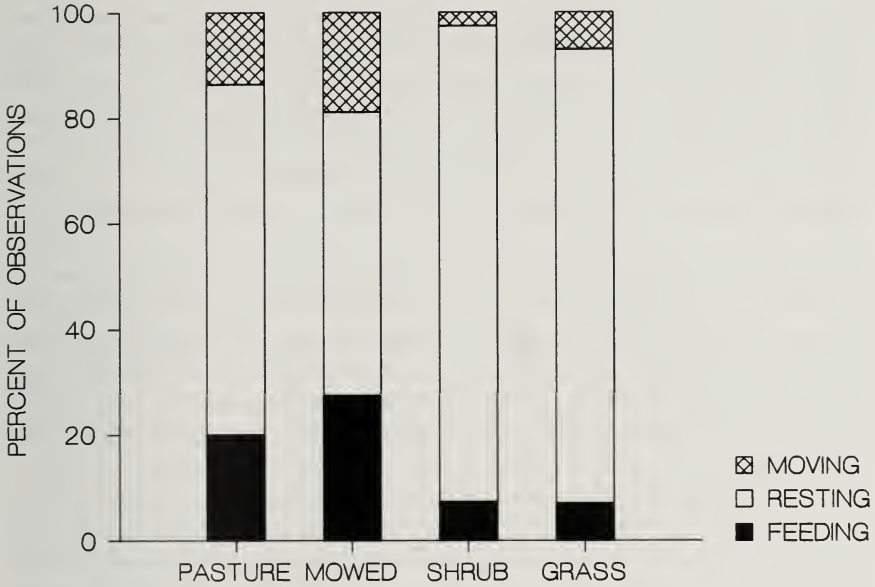

FIG. 3. Percentages of observations during which Common Ravens engaged in various activities in different habitat types, May 1985–February 1987.

tern in feeding was apparent during winter. The proportion of each hour devoted to flying appeared greatest in the late afternoon during spring and in the middle of the day during summer and fall. In contrast, no significant linear trends were apparent in the proportions of hours spent either resting or moving (ANCOVA, Ps > 0.14), and these patterns did not differ significantly among seasons (ANCOVA, Ps > 0.12).

Habitat effects on activity.—The percentages of time ravens devoted to feeding, resting, and moving differed among habitat types (two-way ANOVA, Ps < 0.001; Fig. 3). These differences were similar among seasons (two-way ANOVA, Ps > 0.75): in any given season, ravens spent a higher proportion of the daytime feeding, and less time resting, while in mowed or stubble agricultural fields and pastures than when they were in either shrub or grass habitats (Tukey HSD, Ps < 0.02).

DISCUSSION

Passerine birds have extremely high weight-specific metabolic rates among vertebrates (Lasiewski and Dawson 1967), thus feeding is typically a dominant daytime activity (Schartz and Zimmerman 1971, Fischer 1981). In ravens, however, resting was the predominant daytime activity during all times of year. This difference may be due to the relatively large

body size of the raven and/or the abundant food supply in our study area. The Common Raven is the largest passerine bird (Goodwin 1976), and larger birds tend to spend less time feeding than do smaller ones (Gibb 1954). In addition, the abundant food supply for ravens in our study area (Engel and Young 1989b) may have enabled ravens to devote relatively little time to acquiring food. Food density has been known to influence negatively the amount of time spent feeding by an animal (Pianka 1974)

Seasonal activity budget.—Similar to other passerine birds (Gibb 1956, Verner 1965, Verbeek 1972), ravens exhibited prominent seasonal changes in their activity budgets, the most obvious of which was a dramatic increase in feeding during spring. This springtime hyperphagia was likely due to increased energy demands of breeding activities. Increased day lengths in spring stimulate gonad development in a variety of birds, and the concomitant energy demands are often met by increased feeding (Kendeigh 1941).

Lack of seasonal variation in time engaged in locomotory activities (i.e., flying and moving) may further reflect the perennially abundant concentration of food for ravens in our study area (Engel and Young 1989b). Year-round, ravens in our study area tended to fly to a single foraging area (e.g., cattle feedlot, landfill, or stubble corn field) where they spent the majority of the day before returning to the roost in the evening (Engel 1990). Furthermore, with seasonal times devoted to locomotory activities remaining stable, the springtime decrease in resting suggests an inverse relationship between feeding and resting as observed in Rock Pipits (*Anthus spinoletta*; Gibb 1956).

Although feeding rates and gross energy intake in passerine birds are typically influenced directly by ambient temperature (Seibert 1949) and day length (Gibb 1956), raven feeding rates appeared unaffected by either. Below the thermoneutral zone, temperature regulation in birds requires an increase in metabolism and energy consumption (Calder and King 1974). The lower critical temperature of winter-acclimatized ravens is below −20°C (Schwan and Williams 1978). Mean daily temperatures in our study area, however, were never below −15°C (U.S. Department of Commerce, unpubl. data) and were thus within the lower bounds of the thermoneutral zone for ravens. Similarly, although relatively few daylight hours were available for feeding during winter, ravens spent virtually the same proportion of the daytime feeding during winter as during summer. This apparent lack of influence of day length on raven feeding reflects the ability of ravens to obtain adequate amounts of food on a daily basis in our study area (Engel and Young 1989a, b).

Daily activity budget.—Seasonal variation in daily feeding patterns such as we observed has been described in a variety of birds and is thought to

relate to changes in daily patterns of food availability (Fischer 1981, Boxall and Lein 1989) and ambient temperature (Gibb 1956, Verbeek 1972). Bimodal feeding patterns, in particular, are common in both migratory and non-migratory birds (Baldwin and Kendeigh 1938, Lees 1948, Gibb 1956, Boxall and Lein 1989) and are apparently adaptive for accumulating overnight energy reserves immediately before roosting and then replenishing depleted reserves the following morning (Murton and Westwood 1977).

The bimodal foraging pattern of ravens may have been influenced by crepuscular activity maxima of their main prey species as observed in Snowy Owls (*Nyctea scandia*; Boxall and Lein 1989). Grasshoppers (Orthoptera) were one of the main food sources for ravens in summer and fall (Engel and Young 1989b), and during the heat of the day, grasshoppers were likely less active and thus less obvious to foraging ravens. Uvarov (1977) found that grasshopper activity became depressed at temperatures $\geq 41°C$, which are not uncommon during summer and fall in our study area.

Bimodal feeding patterns of ravens were also likely influenced by relatively high ambient temperatures during mid-day in summer and fall as observed in White-crowned Sparrows (*Zonotrichia leucophrys*; Morton 1967). When ambient temperatures exceed the upper limits of a bird's thermoneutral zone, active regulation of body temperature can become more crucial than foraging (Calder and King 1974); consequently, birds may become less active, seek shade, or fly to higher, cooler altitudes to decrease or maintain acceptable body temperatures. This phenomenon may also explain the increase in flying we observed during mid-day in summer and fall.

Lack of any distinct feeding pattern during winter may have been due to a need to accumulate energy more evenly throughout the day during cold weather. Morton (1967) observed a loss of the bimodal feeding pattern in White-crowned Sparrows during stressful weather.

Habitat effects on activity.—During any given season, ravens primarily fed while on agricultural land and rested while in shrub- or grass-dominated rangelands. These patterns of habitat use were reflected in the composition of the raven diet, a large proportion of which was comprised of food items obtained from agricultural land (Engel and Young 1989b). Food sources for ravens may have been more concentrated or of higher quality in agricultural habitats than in "natural" (i.e., shrub and grass) habitats. Eberhardt et al. (1989) found that Canada Geese (*Branta canadensis*) foraged most often in habitats where food was more concentrated or of higher protein content than in other habitats.

Ravens may have used shrub- or grass-dominated rangelands primarily

for resting because of the protective cover the taller, denser vegetation provides from both the weather and predators. Caraco et al. (1980) found that flocks of the Yellow-eyed Junco (*Junco phaeonotus*) were able to spend less time watching for predators the closer they were to cover.

Overall, raven activity budgets appeared to be strongly influenced by characteristics of food sources in our study area and preparation for reproduction, rather than by age of bird or changes in ambient temperature and day length. Ambient temperature may have influenced daily patterns of activity but not the overall percentages of time devoted to various activities. Therefore, we expect raven activity budgets may differ significantly in areas with less abundant and more dispersed food supplies than in our study area, but that dramatic springtime increases in feeding should occur regardless of locale.

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DIURNAL TIME-ACTIVITY BUDGETS AND HABITAT USE OF RING-NECKED DUCK DUCKLINGS IN NORTHCENTRAL MINNESOTA

STEPHEN J. MAXSON[1] AND RICHARD M. PACE, III[2]

ABSTRACT.—We studied diurnal time-activity budgets and habitat use of 36 individually marked, class II and III Ring-necked Duck (*Aytha collaris*) ducklings during 1983 and 1984 in northcentral Minnesota. Overall, ducklings spent 40.9% of their time foraging, 30.8% resting, 21.0% in comfort activities, 6.0% in locomotion, and 1.3% alert. Within broods, duckling activities were synchronized. When the duckling being sampled was foraging, resting, or engaged in comfort movements, 87%, 77%, and 56%, respectively, of the other brood members were engaged in the same behavior. Although male ducklings were larger than their female siblings, we detected no sex differences in activity budgets, dive rates, or the proportion of time spent in subsurface vs surface feeding. Only time spent in comfort and locomotor activities varied by time of day. Time spent in all activities, except comfort, differed between years. Five of six hens abandoned their broods before the ducklings could fly. Thereafter, ducklings spent more time foraging and less time resting and in comfort activities. Ducklings were never observed on shore. They spent 82.6% of their time in open water, although use of this habitat component was less than its availability (96.7%). While in open water, ducklings spent most of their time foraging (50.9%), resting (20.6%), and in comfort activities (19.2%). Exposed flats, consisting of islands of decayed organic debris, were used (16.0%) far in excess of their availability (0.3%), indicating ducklings actively selected this habitat component where they mostly rested (65.8%) and engaged in comfort activities (28.4%). *Received 9 May 1991, accepted 1 Feb. 1992.*

Time-activity budget studies are useful for quantifying how ducks apportion their time to cope with varying energy demands, how they cope with various environmental changes on a daily, seasonal, and year-to-year basis, and how these birds use habitat. Brood rearing is an important phase in the annual cycle of ducks. Several time-activity budget studies have quantified the behavior of brood hens and/or ducklings (e.g., Hammel 1973, Siegfried et al. 1976, Joyner 1977, Ringelman and Flake 1980, Afton 1983, Hickey and Titman 1983, Paulus 1984, Rushforth Guinn and Batt 1985). However, none of these studies has sampled individually marked ducklings of known sex nor have any time-activity budget studies been conducted on Ring-necked Duck (*Aythya collaris*) broods.

The Ring-necked Duck is a small-bodied diving duck that breeds primarily in the closed boreal forest of Canada. In the United States, the

[1] Wetland Wildlife Populations and Research Group, Minnesota Dept. of Natural Resources, 102 23rd St., Bemidji, Minnesota 56601.
[2] Wildlife Populations and Research Unit, Minnesota Dept. of Natural Resources, 500 Lafayette Road, St. Paul, Minnesota 55155. (Present address: U.S. Fish and Wildlife Service, Louisiana Cooperative Fish and Wildlife Research Unit, Forestry, Wildlife and Fisheries Building, Louisiana State Univ., Baton Rouge, Louisiana 70803.)

largest numbers are found in the Great Lakes states (Bellrose 1976), and it has been estimated to be the second most abundant breeding duck in the forested areas of Minnesota (Moyle 1964). Male Ring-necked Ducks weigh more than females except during the ovulation and laying periods (Hohman et al. 1988, Hier 1989). Because standard metabolic rates are a function of body mass, a larger bird must expend more energy (and thus require more food) to conduct any given activity than a smaller bird. If the sexual size dimorphism is also present in ducklings it should contribute to corresponding differences in time-activity budgets, especially with regard to foraging. These might be expressed as differences in total time spent foraging, the proportion of time spent in subsurface versus surface foraging, or in diving rates.

Male and female Ring-necked Ducks experience different selection pressures as reflected in higher survival rates of males (Conroy and Eberhardt 1983). This results in adult sex ratios skewed in favor of males (Mendall 1958, Bellrose et al. 1961, Jahn and Hunt 1964, Anderson et al. 1969). The sexes also have differing reproductive strategies with regard to time and energy expenditure (Hohman 1984). Intersexual differences in survival and reproductive strategies might be evident as early as the duckling stage and could be reflected in time-activity budgets.

Diving duck hens frequently abandon their broods before the ducklings can fly (Hochbaum 1944). Whether Ring-necked Duck ducklings alter their time-activity budgets after hens depart is unknown. How Ring-necked Duck broods modify time-activity budgets during the day or between years is also unknown. Habitat use by Ring-necked Duck broods has not been quantified.

We documented diurnal time-activity budgets and habitat use of Ring-necked Duck ducklings during age classes IIb–III (i.e., ducklings 25–60 days of age) (Larson and Taber 1980) and determined whether time-activity budgets differed by sex, time of day, or year and whether the hen was present with the brood. We quantified the degree of behavioral synchrony among brood members. We also documented dive rates and the ratio of subsurface to surface feeding by ducklings to determine whether these differed between sexes.

STUDY AREA AND METHODS

Broods were observed at Refuge Pond, a 45-ha wetland 7 km northeast of Bemidji, Minnesota. This wetland was also used by broods of Mallards (*Anas platyrhynchos*), Blue-winged Teal (*A. discors*), Wood Ducks (*Aix sponsa*), and Common Goldeneyes (*Bucephala clangula*). The wetland is a permanently flooded aquatic bed in a lacustrine system (Cowardin et al. 1979). A 25-ha floating mat of sedge (*Carex* spp.) and cattail (*Typha latifolia*) covered the northwest portion of the basin. The remainder of the wetland (20 ha) was largely open water.

We overlaid a grid on aerial photos of the wetland to quantify the proportion of each habitat component. Because we did not observe Ring-necked Duck broods using the floating mat portion of the wetland, we included only the open portion of the basin in our analysis. Most of this area was classified as open water. Water depth was ≤1.5 m. Aquatic plants were abundant in this zone and were dominated by large leaf pondweed (*Potamogeton amplifolius*), floating leaf pondweed (*P. natans*), white waterlily (*Nymphaea tuberosa*), and water shield (*Brasenia schreberi*). Hardstem bulrush (*Scirpus acutus*) was scattered throughout the open water zone but was too sparse to warrant a separate classification. Remaining habitat components included stands of cattail, stands of hardstem bulrush, small islands of floating sedge/cattail mat, and exposed flats consisting of islands of decayed organic debris.

Ring-necked Duck ducklings were captured by nightlighting (Lindmeier and Jessen 1961), sexed (Addy and MacNamara 1948), aged (Larson and Taber 1980), weighed, and banded with a U.S. Fish and Wildlife Service aluminum leg band. We also fitted each with a nasal saddle (Sugden and Poston 1968) coded to allow individual identification. Observations began two days after capture, allowing broods to reassemble and ducklings to habituate to nasal saddles.

Ducklings were observed with binoculars and an 80× telescope from a vehicle on a hill overlooking the wetland. Data were collected during 1-h sampling periods between 4 Aug.–14 Sept. 1983 and 8 Aug.–13 Sept. 1984. We conducted 1–4 sample periods ($\bar{x}$ = 1.9) per day. Duckling activities and habitat use were recorded by instantaneous sampling (Altmann 1974) at 15-sec intervals at the tone of a metronome (Wiens et al. 1970). Activities were classified as: foraging, resting, comfort movements, locomotion, alert, and agonistic behaviors (Johnsgard 1965). Foraging included dives, dive-pauses, and surface feeding (dabbling and food-handling). Dive-pauses typically lasted only a few sec. Pauses lasting more than 15 sec were classified as alert or resting. Comfort movements included preening, bathing, stretching, wing flapping, or scratching (McKinney 1965). Locomotion included swimming not primarily associated with foraging, walking, and flying. During each sampling period, one duckling was observed for 30 min and a second duckling, usually within the same brood, was observed for the remaining 30 min. When possible, both sexes were observed during a sampling period. We alternated which sex was observed first and varied the individuals sampled. The day was divided into four time (CDT) blocks (1 = dawn–10:00, 2 = 10:01–14:00, 3 = 14:01–18:00, 4 = 18:00–dusk). Within each time block, the start of sampling was varied from day to day so that all daylight hours were sampled over the course of the study. We also recorded whether the sample took place prior to (hen present) or after (hen absent) a hen permanently abandoned her brood. Although duck hens sometimes leave their broods for short periods (e.g., Afton 1983, Paulus 1984), none of our samples were recorded during temporary absences.

During sampling periods, we documented behavioral synchrony among brood members by recording the activity of the focal bird at 2.5-min intervals and then scanning the other brood members and recording their activity. These data were only collected from ducklings that were still accompanied by the brood hen, because after hens departed, broods became less clumped spatially, making instantaneous scans difficult.

The sampling unit for activity budget analyses was one 30-min period. For each sampling unit, the number of instances of each activity was summed and converted to percent of time. To insure homogeneity of variance, the arcsin square root transformation (Anderson and McLean 1974) was applied to data before analysis. We estimated components affecting the variance of each activity using maximum likelihood methods with the BMDP3V program for general mixed ANOVAs (Jennrich and Sampson 1976). Our model consisted of a fixed component for the overall mean, another fixed component for the sex by time of day, by year, by hen presence category that described each datum, and three random components

representing three levels of sampling (i.e., broods, individuals within a brood, and repeated observations on an individual duckling). We tested the hypotheses that the variance attributable to broods and individuals was zero. These variance components did not appear to contribute significantly (no $P < 0.25$) to total variance. Therefore, we collapsed our original model to one that included only a single random component (replicates within a sex by time of day, by year, and by hen presence cell) and analyzed observed activities with more traditional MANOVA and ANOVA least squares models using the GLM procedure of the Statistical Analysis System (Helwig and Council 1979). Least square estimates of the various means were determined from the appropriate models and are reported as retransformed values.

To compare the relative amounts of time spent in surface foraging versus subsurface foraging (dive plus dive-pause), we subjectively omitted sampling units having fewer than 15 data points in the forage category to eliminate samples covering only a small portion of a foraging bout (foraging bouts typically lasted 15–25 min). For the remaining sampling units, we analyzed the proportion of foraging time spent in subsurface foraging using a least squares analysis of means model (Searle 1987). We tested 10 simple contrasts that accounted for as much of the four main effects (sex, year, time of day, hen presence) and all two-way interactions that missing cell means (6 of 32 cells) would permit. Prior to analysis the arcsin square root transformation was applied to these data.

When feasible, we also recorded the total number of dives by the focal bird during the 30 min it was sampled. Dive rates (the number of dives per 15-sec interval during subsurface foraging bouts) were calculated by dividing the total number of dives by the combined data points in the dive and dive-pause categories. We chose to omit from analysis sampling units having fewer than 10 data points in the combined dive and dive-pause categories. We used a paired *t*-test (Snedecor and Cochran 1980) to compare dive rates between sexes for those sampling periods when dive rate data were obtained from both sexes.

RESULTS

Activity and habitat use data were obtained from 36 ducklings (18 male, 18 female) from six broods. We obtained 135 30-min samples from males and 104 samples from females. Individual ducklings were sampled from 1–33 times (median = 5).

Activity budgets.—Overall, Ring-necked Duck ducklings averaged 40.9% of their time foraging, 30.8% resting, 21.0% in comfort activities, 6.0% in locomotion, and 1.3% alert (Table 1). Agonistic activities occurred rarely (<0.1% of the time) and were not analyzed statistically.

Broods often synchronized their activities (Table 2). Synchrony was most pronounced during foraging and resting as most of the other brood members foraged or rested at the same time as the focal bird. Comfort activities were less synchronized indicating that comfort activities also occurred when other brood members were foraging or resting.

Within broods, mean female weights at capture ranged from 77–96% of mean male weights. No female weighed more than any of her male siblings. However, tests for differences among activity budgets indicated no significant effects for sex or any interacting set of effects that included sex. Consequently, we omitted sex as an explanatory variable and reran

MANOVAs on the remaining three variables. The Wilk's Lambda test criterion indicated significant overall effects for time of day ($F = 2.31$, df = 15, 605, $P = 0.0033$), year ($F = 6.73$, df = 5, 219, $P = 0.0001$), hen presence ($F = 3.99$, df = 5, 219, $P = 0.0018$), and the interaction between time of day and year ($F = 2.06$, df = 15, 605, $P = 0.0103$). No overall effects were indicated for the year by hen presence ($F = 1.84$, df = 5, 219, $P = 0.1059$), time of day by hen presence ($F = 0.82$, df = 15, 605, $P = 0.6518$), or the year by time of day by hen presence ($F = 1.59$, df = 15, 605, $P = 0.0705$) interactions. We used three-way ANOVAs to identify which activities were influenced by these overall effects.

Only time spent in comfort activities ($F = 4.49$, df = 3, 223, $P = 0.0044$) and locomotion ($F = 7.04$, df = 3, 223, $P = 0.0002$) differed by time of day. Comfort activities occurred most often during period 3 and least often during period 4 (Table 1). Locomotion was highest during period 3 and lowest during period 2.

Time spent in all activities except comfort differed between years (Table 1). Ducklings spent more time foraging in 1983 than 1984 ($F = 13.06$, df = 1, 223, $P = 0.0004$). Conversely, they spent more time resting in 1984 ($F = 12.78$, df = 1, 223, $P = 0.0004$). More locomotion ($F = 14.67$, df = 1, 223, $P = 0.0002$) and alert ($F = 8.88$, df = 1, 223, $P = 0.0032$) were observed in 1983.

We found a significant interaction between time of day and year for resting ($F = 3.10$, df = 3, 223, $P = 0.0278$), locomotion ($F = 5.03$, df = 3, 223, $P = 0.0021$), and alert ($F = 3.18$, df = 3, 223, $P = 0.0250$). Whereas resting occurred least often in time periods 2 and 4 in 1983, resting occurred most often during these periods in 1984 (Table 1). In 1983, locomotion showed an increasing trend from time periods 1 to 3. However, in 1984 there was a sharp decline in locomotion between time periods 1 and 2. Alert showed an increasing trend throughout the day in 1983 but in 1984 showed decreases in time period 2 and especially period 4.

All six brood hens abandoned their ducklings during the study period. One left two days after her ducklings achieved flight capability. The other hens departed 3, 4, 8, 10, and 19 days before their ducklings could fly. These departures did not appear related to the disturbance caused by nightlighting operations as hens departed an average of 12.2 days after their ducklings were captured. Typically, ducklings remained together as a brood for the first few days after being abandoned. Gradually, they became more independent and spread out more widely on the pond. Ducklings began making short flights when two months old and dispersed from the pond 2–5 days later.

After hens abandoned their broods, ducklings spent more time foraging

TABLE 1

MEAN PERCENTAGE OF TIME DUCKLINGS SPENT IN EACH ACTIVITY BY TIME OF DAY AND YEAR[a]

Time period[b]	N[c]		Forage			Comfort			Rest			Locomotion			Alert		
	1983	1984	1983	1984	Mean	1983	1984	Mean	1983	1984	Mean	1983	1984	Mean	1983	1984	Mean
1	32	20	43.5	41.3	42.4	22.0	22.6	22.3	25.3	30.9	28.1	7.7	4.2	6.0	1.5	0.8	1.2
2	45	29	51.2	26.2	38.7	18.9	18.8	18.8	20.3	52.8	36.6	7.9	1.9	4.9	1.5	0.4	1.0
3	39	24	38.4	35.9	37.2	26.1	25.4	25.8	24.2	31.1	27.7	9.1	6.1	7.6	2.1	1.2	1.7
4	31	19	58.7	31.7	45.2	16.6	17.1	16.9	12.9	48.3	30.6	8.6	2.6	5.6	3.0	0.3	1.7
Mean			48.0	33.8	40.9	20.9	21.0	21.0	20.7	40.8	30.8	8.4	3.7	6.0	2.0	0.7	1.3

[a] Original analyses were conducted using arcsin transformed proportions. Depicted values are retransformed least squares means from the appropriate model.
[b] 1 = dawn–10:00, 2 = 10:01–14:00, 3 = 14:01–18:00, 4 = 18:01–dusk.
[c] Number of 30-min samples.

TABLE 2

COMPARISON OF ACTIVITIES BETWEEN SAMPLE BIRDS AND OTHER BROOD MEMBERS

Activity of sample bird	N[a]		Activity (%) of other brood members			
	Sample bird	Brood members	Foraging	Comfort	Rest	Locomotion
Foraging	100	643	87.3	6.8	5.1	0.8
Resting	100	638	3.3	17.1	77.7	1.9
Comfort	58	366	22.9	56.0	18.6	2.5

[a] Number of data points obtained at 2.5-min intervals during samples.

($F = 14.31$, df = 1, 223, $P = 0.0002$) and less time in comfort ($F = 10.26$, df = 1, 223, $P = 0.0016$) and resting ($F = 7.49$, df = 1, 223, $P = 0.0067$) than they did while the hen was present (Table 3). Time spent in locomotion and alert remained unchanged.

We had 104 30-min samples for contrast analyses of subsurface versus surface foraging. No sex or time of day differences were found. The only explanatory variables making significant contributions toward overall variance in the proportion of foraging time spent in subsurface foraging were year ($F = 25.49$, df = 1, 78, $P = 0.0001$) and year by hen presence interactions ($F = 8.46$, df = 1, 78, $P = 0.0047$). Therefore, we ran an ANOVA model to produce estimates of means for the year by hen presence interaction. These indicated that the effect of the brood hen's presence was greater in 1984 than in 1983. After brood hens departed in 1983, ducklings spent a somewhat greater proportion of their foraging time in subsurface foraging (77.1%—present vs 95.8%—absent). However, in 1984 the proportion of subsurface foraging decreased markedly after brood hens departed (93.6%—present vs 49.1%—absent).

TABLE 3

MEAN PERCENTAGE OF TIME DUCKLINGS SPENT IN EACH ACTIVITY WHEN THE BROOD HEN WAS PRESENT OR ABSENT[a]

Activity	Hen present	Hen absent
Foraging	32.2	49.6
Comfort	23.6	18.3
Rest	37.2	24.4
Locomotion	6.0	6.0
Alert	1.0	1.7
N[b]	98	141

[a] Original analyses were conducted using arcsine-transformed proportions. Depicted values are retransformed least squares means from the appropriate model.

[b] Number of 30-min samples.

TABLE 4

RING-NECKED DUCK DUCKLING HABITAT USE VS AVAILABILITY AND DUCKLING TIME-ACTIVITY BUDGETS WITHIN EACH HABITAT COMPONENT ON REFUGE POND

Habitat component	Availability (%)	Use (%)	N[a]	Activity within habitats (%)				
				Foraging	Comfort	Rest	Locomotion	Alert
Open water	96.7	82.6	23,562	50.9	19.2	20.6	7.7	1.6
Exposed flat	0.3	16.0	4570	3.5	28.4	65.8	1.1	1.3
Bulrush stand	0.9	1.1	313	92.0	5.8	0.6	0.6	1.0
Floating mat island	0.7	0.3	82	0.0	50.0	48.8	0.2	0.0
Cattail stand	1.4	0.0	0	0.0	0.0	0.0	0.0	0.0

[a] Number of instances focal ducklings were recorded in each habitat component.

We recorded 5043 foraging dives during 98 30-min sampling units. The overall mean dive rate was 0.874 ± 0.181(SD) dives per 15-sec interval. For 15 sampling periods in which data were obtained from both sexes, dive rates did not differ by sex ($t = 2.01$, df = 14, $P = 0.0637$).

Habitat use.—Mineral soil made up 77% of the shoreline of the pond while floating sedge/cattail mat comprised the remainder. However, ducklings were never observed on shore nor were they ever observed in cattail stands along the pond edge. Bulrush stands and small floating sedge/cattail mat islands appeared to be used in proportion to their availability (Table 4). Ducklings spent the great majority of their time in open water, although use of this habitat component was somewhat less than its availability. Exposed flats were used far in excess of their availability, indicating that broods actively sought out this habitat component.

Ducklings used open water primarily for foraging, but substantial amounts of comfort and resting occurred there as well (Table 4). The small amount of time spent in bulrush stands was almost exclusively used for foraging. On the other hand, exposed flats and floating sedge/cattail mat islands were used primarily for resting and comfort activities.

DISCUSSION

Because of the sexual size dimorphism and differing intersex survival and reproductive strategies exhibited by adult Ring-necked Ducks, it can be argued that sex differences should be evident from the time of hatching. This appears to be the case with regard to size dimorphism but not in other aspects. Compared to other stages in their life cycle, ducklings of both sexes experience relatively similar energy demands associated with growth and development. At this stage, intersex energy budget comparisons are not complicated by differential costs of courtship, gamete pro-

duction, molt, etc. Major activities among brood members were synchronized, and both sexes foraged together in the same habitats, further indicating that intersex survival strategies are not markedly different during this period. Nevertheless, based on the size difference alone, we expected to find sex differences in time-activity budgets particularly associated with foraging. However, we detected no significant differences in activity budgets based on sex, nor did we find sex differences in the proportion of foraging time spent in subsurface versus surface feeding or in diving rates. Several factors may have accounted for this. The range of duckling age (and thus different mass) over which we sampled may have obscured subtle sex differences in foraging time or technique. Additionally, our most direct comparison (dive rates) had a small sample size and thus low power. Further, males may have selected a slightly different diet than females or there could have been sex differences in nocturnal activity. We were unable to measure either of these factors.

Most time-activity budget studies of ducklings have noted behavioral changes during the day, especially with regard to foraging. Early morning and late afternoon peaks in foraging have been reported for Blue-winged Teal, Mallard, and Ruddy Duck (*Oxyura jamaicensis*) ducklings (Joyner 1977, Ringelman and Flake 1980). Mottled Duck (*Anas fulvigula*) ducklings foraged most in the morning and less during midday before increasing foraging at night (Paulus 1984). Mendall (1958), though lacking quantitative data, reported that Ring-necked Duck broods tended to be more active in morning and evening but that feeding and resting periods occurred frequently throughout the day with little evidence of fixed routines. In contrast, we did not detect differences in time spent foraging throughout the daylight hours. Furthermore, time of day differences in resting, locomotion, and alert were inconsistent between years. The extent Ring-necked Duck duckling time-activity budgets change at night is unknown. During nightlighting operations, Minnesota Dept. of Natural Resources duck banding crews frequently observe broods of Ring-necked Ducks foraging (R. T. Eberhardt, pers. comm.).

Differences between years for all activities except comfort were likely related to changes in food abundance or availability on the pond. During age classes II and III, Ring-necked Duck ducklings eat a variety of plants and animals (Mendall 1958, Hohman 1985, McAuley and Longcore 1988). Although juvenile Ring-necked Ducks exhibit preferences for certain foods, availability plays a prominent role in food selection (Hohman 1985). Hohman (1984, 1985) noted year-to-year changes in foods available to Ring-necked Ducks and found that contributions of individual food species in class II Ring-necked Duck duckling diets differed between years

in northwestern Minnesota. If one assumes that nutritional needs of class II and III ducklings remain the same from year to year and that ducklings attempt to forage efficiently, then the amount of time spent foraging at any particular stage of their development should be a function of food abundance or availability. As sufficient food becomes easier to obtain, less foraging time is required. Relationships between food levels and the amount of time spent foraging have been noted in other waterfowl (Paulus 1988) as well as in non-waterfowl species (e.g., Maxson and Oring 1980). The only notable environmental difference between years was that August pond levels were 16.5 cm lower in 1984. This was the lowest August water level recorded on the pond during the 1979–1984 period (R. T. Eberhardt, unpubl. data) and it may have influenced abundance or availability of duckling foods. Further evidence of changes in foods was the fact that duckling foraging tactics differed between years. In 1984, particularly during the period after brood hens departed, ducklings spent considerably more time surface feeding (primarily dabbling) than during other phases of our study.

Given that time is limited, any change in time spent in one activity must be reflected in a corresponding change in time spent in other activities. We believe that the driving factors determining duckling time-activity budgets were requirements for foraging and feather maintenance, and that, in general, other activities (especially resting) filled in any time gaps remaining after these needs had been met. Time spent in comfort activities did not differ between years, likely because a certain proportion of time is required for feather maintenance regardless of other factors. When foraging time decreased in 1984, this time gap was compensated for primarily by increased time spent resting. An inverse relationship between time spent foraging and resting has also been noted in other waterfowl (Paulus 1988). The greater amount of time spent in locomotion in 1983 was associated with the higher foraging and alert time that year. Locomotion was recorded primarily as broods travelled between foraging sites, between foraging and loafing sites, or as they moved away from potential predators.

After hens abandoned their broods, ducklings spent more time foraging while spending less time resting and in comfort activities. Several explanations are possible. As ducklings approach adult size they require increased amounts of food based on the increase in their body mass alone. Without the hen to help guide them to good feeding locations, ducklings may initially be less efficient in finding sufficient food, although this may entail only a minor behavioral adjustment as ducklings had already been foraging on the pond 40–60 days. Also, there may have been some late

season changes in food abundance or availability resulting in increased foraging time. These explanations are not mutually exclusive and all three may have been in operation.

Although ducklings spent a smaller proportion of their time in open water than its percent availability on the pond, it is difficult to conclude that a habitat component used >80% of the time was not selected for. Indeed, ducklings did almost all of their foraging, as well as the majority of their resting and comfort activities, in open water. The only habitat component actively selected, relative to its availability, was exposed flats which ducklings used for resting and comfort activities. The fact that ducklings were never observed on shore suggests that they may have felt more secure in open areas away from dense vegetation. In this regard, exposed flats were located well away from shorelines or other heavily vegetated areas and offered broods easy access while affording an unrestricted view. By contrast, floating cattail/sedge mat islands, which had a similar availability but were seldom used, were well vegetated, were more difficult for ducklings to access, and afforded a much more restricted view of the surroundings.

The habitat use values that we recorded would be expected to vary somewhat among wetlands, depending on the availability and distribution of habitat components. Nevertheless, our data suggest that class II–III Ring-necked Duck broods have a preference for open portions of wetlands.

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AVIAN HABITAT ASSOCIATIONS IN RIPARIAN ZONES OF IDAHO'S CENTENNIAL MOUNTAINS

David C. Douglas,[1] John T. Ratti,[2] R. Alan Black,[3] and J. Richard Alldredge[4]

Abstract.—Patterns of bird distribution within riparian habitat of the Centennial Mountains, Idaho, were investigated during the summers of 1983–1984. Avian habitat use, vegetative structure, and saturated soil coverage were surveyed in 98, 0.25-ha plots. Avian abundance distributions and habitat relationships were plotted and compared with reciprocal averaging and canonical correlation analyses. Use of riparian habitats by avian species was non-random and indicated a correlation with vegetative structure, life form, and soil moisture. Canonical correlation analysis revealed that avian distributions paralleled a moisture gradient. Our results allow assessment of impacts on avian populations by environmental perturbations causing vegetative-structure and composition, or soil-moisture changes to riparian systems. These data indicate that subtle changes to riparian areas (e.g., from cattle grazing, timber harvest, drainage, etc.) may have severe impacts on the bird community. *Received 9 July 1991, accepted 12 Feb. 1992.*

Riparian habitats in western regions are severely threatened by numerous environmental perturbations, including development, forest-cutting practices, flood control, agriculture, grazing, and pollution (Kusler 1985). "Riparian vegetation has been referred to as the aorta of an ecosystem because of its significance to the perpetuation of water, fish, wildlife, rangeland, and forest resources" (Knopf and Samson 1988:77). Knopf and Samson (1988) also note that <1% of the western United States contains riparian vegetation, yet these habitats are used by more species of breeding birds than any other habitat type in North America. Detailed information on the various components of riparian ecosystems is needed to manage riparian habitats (Platts et al. 1987).

Bird distribution is often related to vegetative characteristics or habitat types, which are a subset of the overall "niche gestalt" (James 1971). Vegetative structure may provide proximal factors for habitat selection (Hilden 1965). In turn, this habitat selection process provides ultimate factors such as food, nest sites, and protection from predators (Hilden 1965, Balda 1975). Causal relationships between habitats and birds are difficult to determine, since habitat characteristics perceived by bird species for habitat selection are usually unknown, and analyses of field data only reveal correlations or associations (Johnson 1981a, Karr 1981).

[1] Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service, 1011 E. Tudor Rd., Anchorage, Alaska 99503.
[2] Dept. of Fish and Wildlife Resources, Univ. of Idaho, Moscow, Idaho 83843.
[3] Dept. of Botany, Washington State Univ., Pullman, Washington 99164-4238.
[4] Program in Statistics, Washington State Univ., Pullman, Washington 99164-6212.

Examinations of avian-habitat relationships often have incorporated aspects of vegetative structure and plant species composition, which then are correlated with bird community structure (Carothers et al. 1974, Willson 1974, Stamp 1978, Stauffer and Best 1980, Meents et al. 1981) or with the abundance of singing males (James 1971, Whitmore 1975, Smith 1977). Moisture gradients and vegetative physiognomy also may be correlated with avian distribution (Smith 1977, Swift et al. 1984). Interactions of water with various physical characteristics of the environment (e.g., topography, soil, elevation) contribute to the diversity of riparian vegetation (Thomas et al. 1979). Furthermore, riparian ecosystems are highly productive and support a greater faunal diversity when compared to adjacent uplands (Odum 1978).

Our objectives were to sample and analyze avian habitat use within the riparian zones of the Centennial Mountains, and to sample and describe riparian habitat gradients and examine distributions of avian abundance among habitats. We sought to determine if different physiognomic characteristics within the riparian zone reflected different use of various riparian habitats by bird species.

STUDY AREA AND METHODS

The study was conducted in the eastern portion of the Centennial Mountains, Fremont and Clark counties, Idaho (see maps in Douglas and Ratti 1984). Elevation on the study area ranged from approximately 1860 to 1940 m. Lodgepole pine (*Pinus contorta*) was the most abundant tree species, and forest stands had extensive mountain pine beetle (*Dendroctonus ponderosae*) infestation. Engelmann spruce (*Picea engelmannii*) and Douglas-fir (*Pseudotsuga menziesii*) dominated narrow, V-shaped drainages. Quaking aspen (*Populus tremuloides*) occurred in small stands along lower slopes. Willows (*Salix myrtillifolia, S. drummondiana, S. geyeriana, S. wolfii,* and *S. phylicifolia*) dominated shrub communities. Willow communities were found at moist sites, and understory composition ranged from relatively xerophytic mixed graminoids and forbs to mesophytic *Carex* spp. Many sites with saturated soils were occupied entirely by water sedge (*Carex aquatilis*), Ross sedge (*C. rostrata*), and short-beaked sedge (*C. simulata*) and did not support woody vegetation. Beaver (*Castor canadensis*) dams caused inundation of portions of the riparian zone.

Plot establishment.—During May and June 1983, 98 study plots were established within 20 riparian drainages described by Youngblood et al. (1985). Plots (35 × 71.5 m, 0.25 ha) were placed at 250-m intervals with the long axis parallel to the general compass bearing of the drainage. Plots were randomly placed perpendicular to the drainage within the riparian zone. A maximum of three plots was placed in drainages with homogeneous vegetative composition, i.e., as opposed to most drainages with heterogeneous vegetative communities. This method was devised to prevent excess sampling of one vegetative type in a large drainage and to provide relatively representative sampling of drainages with widely varying lengths and widths.

Avian censusing.—Each plot was censused six times in 1983 and twice in 1984 by one observer for 30 min between sunrise and noon. Presence, number, and location of all individuals of all bird species were recorded. Censusing occurred daily during 10-day intervals separated by four days from 8 June through 21 July 1983, and from 5 July through

2 September 1984 (late spring snow melt prevented June censusing in 1984). Observers and census times were rotated among plots within the sampling periods. Bird observations were classified by vegetative substrate (i.e., habitat components) as conifer, aspen, snag, willow, dry meadow, moist meadow, bog, in or adjacent to water, flight, and "other." Relative percent of observations was calculated for both the habitat components (e.g., snags) and the habitat regions (see Results, e.g., conifer-dominated) by dividing the total number of observations in each category for each species by the total number of observations for each species (×100). Unidentified birds or birds flying over a plot were omitted from the analyses. We were careful to record specific individual birds only once on each plot. Birds were not censused during periods of severe wind or rain (Robbins 1981).

Vegetation sampling.—Plots were sampled for vegetative volume during July and August (89 plots in 1983, 9 in 1984). Higher elevation plots were sampled later in the season to record greatest vegetation cover. Vegetative volume of all plant species and the volumes of the two dominant species (>5% cover) were measured at 0.3, 0.9, 1.8, and 3.0 m using coverboard techniques (MacArthur and MacArthur 1961, Hayes et al. 1981) at 16 systematically positioned points within each plot (transects originating at each point were alternated and evenly distributed among cardinal directions). Foliage volume was recorded as zero for a given sample point and height if the distance between the observer and coverboard was >15.2. Eight volume variables were calculated from the data for each plot: (1) low graminoid (0.3 m), (2) high graminoid (0.9 m), (3) low forb (0.3 m), (4) high forb (0.9 m), (5) low willow (0.3 + 0.9 m), (6) high willow (1.8 + 3.0 m), (7) low conifer (0.3 + 0.9 m), and (8) high conifer (1.8 + 3.0 m). Saturated soil was estimated within a 1-m^2 quadrate centered in each sample plot and was recorded as saturated or not saturated. Soils were considered saturated if water ran into a depression made by a bootprint.

Data analyses.—A reciprocal averaging algorithm (RA) (Hill 1973) in the program ORDIFLEX (Gauch 1977) was used to position the 98 plots along multifactorial habitat gradients from square root-transformed variables. Reciprocal averaging is considered superior to principal component analysis (PCA) for data sets containing long community gradients (Gauch 1982). Study plot scores and habitat variable scores found by RA will maximize the correlation between them. Study plots were graphed across the first RA axes based on their ordination scores. Plots most similar with respect to habitat variables were positioned relatively closely, i.e., the degree of dissimilarity among plots was reflected by increasing separations. Environmental interpretation of two-dimensional habitat space was investigated by plotting values of the original habitat variables across the RA axes. This led to a subjective partitioning of six general riparian habitat regions (see Results). The regions represent riparian vegetative communities and were characterized by averaging the habitat variables across study plots located within each partitioned area.

Percents of observations of avian species using each study plot was superimposed onto the habitat space. Percentages were summed within each of the six habitat regions and then proportioned into the environmental categories corresponding to the bird's location when initially observed (e.g., conifer, willow, snag, bog, etc.).

The Shannon-Weaver information equation (Shannon and Weaver 1949) was used to measure habitat breadth for each bird species for the six habitat regions (Johnson 1977). The proportions of avian observations were not scaled with respect to the number of study plots in each region. Thus, habitat breadths were not escalated for species regularly using abundant habitats (Rotenberry and Wiens 1980).

Avian relative frequency (percentages) values and the nine habitat variables were square-root transformed and used in a canonical correlation analysis (CCA) for all plots (Hotelling 1936). Interpretations of habitat canonical variates were derived from correlations with original habitat variables (Levine 1977, Gittens 1979, Smith 1981).

TABLE 1

HABITAT BREADTH[a] AND PERCENTAGE[b] OF BIRD OBSERVATIONS IN RIPARIAN HABITAT REGIONS OF THE CENTENNIAL MOUNTAINS, IDAHO, SUMMER 1983–1984

Species (N)	Habitat breadth	Habitat regions[c]					
		I	II	III	IV	V	VI
Common Snipe (89)	1.48	2.3	10.1	10.1	23.6	10.1	43.8
Red-naped Sapsucker (46)	0.89	0	6.5	26.1	0	65.2	2.2
Willow Flycatcher (65)	0.94	0	0	15.4	0	60.0	24.6
Tree Swallow (655)	1.34	0.1	7.0	7.2	9.2	40.0	36.5
Mountain Chickadee (84)	1.36	28.6	11.9	40.5	2.4	16.6	0
American Robin (237)	1.44	11.4	7.2	23.2	1.7	45.6	10.9
Warbling Vireo (104)	0.95	8.7	0	12.5	0	69.2	9.6
Yellow Warbler (436)	1.16	0.2	3.2	16.7	1.6	54.4	23.9
Yellow-rumped Warbler (105)	1.43	30.5	15.2	25.7	0	26.7	1.9
MacGillivray's Warbler (71)	0.77	2.8	0	26.8	0	69.0	1.4
Common Yellowthroat (169)	0.57	0	0	3.0	4.1	7.7	85.2
Wilson's Warbler (109)	0.86	1.8	0	12.9	0	70.6	14.7
Western Tanager (66)	1.36	33.3	10.6	37.9	0	15.2	3.0
Song Sparrow (116)	0.97	0	1.7	19.0	0	16.4	62.9
Lincoln's Sparrow (496)	1.55	3.4	10.9	22.6	4.2	28.8	30.1
White-crowned Sparrow (227)	0.96	4.4	0	18.9	0	66.1	10.6
Dark-eyed Junco (152)	1.37	34.9	12.5	40.1	1.3	8.6	2.6
Red-winged Blackbird (329)	1.33	0	11.3	17.9	23.7	1.8	45.3
Brown-headed Cowbird (90)	1.53	13.3	5.6	23.3	1.1	32.2	24.5
Pine Siskin (462)	1.34	18.0	1.9	29.9	0	40.0	10.2

[a] Shannon-Weaver (1949) index.
[b] The number of observations in each habitat component divided by N for each species × 100.
[c] I = conifer dominated, II = mesic meadow/conifer edge, III = composite communities, IV = mesic meadow, V = tall willow/xeric, and VI = short willow/mesic.

Consistency among observers, and between-year variation of habitat use by avian species, and study-plot use by individual species was investigated. To test for differences among three observers in the 1983 census, counts for 20 of the most abundant species (Table 1) were divided by the total number of birds observed, arc-sine transformed, and subjected to multivariate analysis of variance (Morrison 1976). Annual change in avian habitat use was investigated using the McNemar test (Conover 1980) and data from 81 plots sampled by a single observer (DCD) in 1983 and 1984. Sorenson's similarity index (Sorenson 1948, in Mueller-Dombois and Ellenberg 1974) was used to test for differences in an individual species' use of study plots between years. To test these differences, the original similarity index was compared to the distribution of 100 indices generated from random subsets of the original data (Garratt and Steinhorst 1976, Lawlor 1980). Statistical tests were judged significant with alpha levels <0.05.

RESULTS

We obtained 4817 observations of 77 bird species. However, we restricted our statistical analysis to 20 species that were observed during

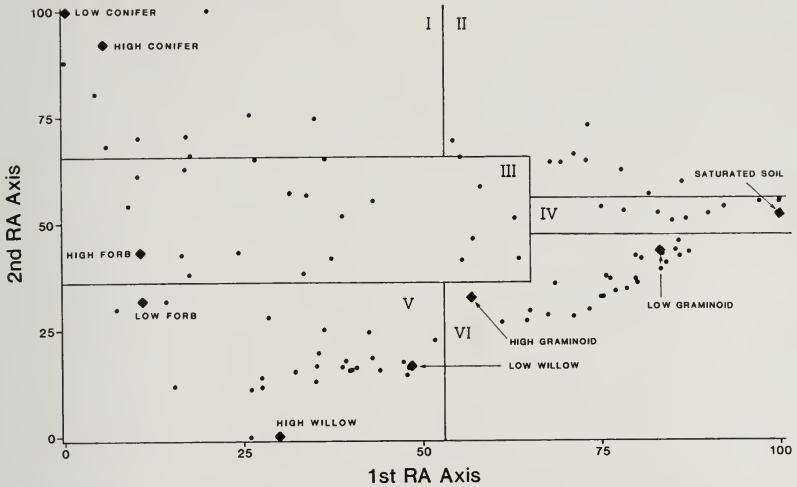

FIG. 1. Ordination of study plots (dots) and habitat variables by reciprocal averaging of riparian zones, Centennial Mountain, Idaho, 1983 and 1984. Regions were classified as : I = conifer dominated, II = mesic meadow/conifer edge, III = composite communities, IV = mesic meadow, V = tall willow/xeric, and VI = short willow/mesic.

>2 census periods on >10 plots (Table 1). This restriction insured adequate sample size for analysis and eliminated rare or transient species.

Environmental gradients.—The first RA axis, primarily a moisture gradient, accounted for 41.4% of the total variation in vegetative structure (Fig. 1). The second RA axis explained an additional 28.3% of variation and separated communities dominated by conifer and willow. Other axes were not considered in the analysis. The habitat variables were positioned along an inverted arch (Fig. 1) that resulted from non-linear relationships among the variables (Phillips 1978, Gauch 1982, Meents et al. 1981). Although the second axis does not convey information independent of the first axis, its inclusion in the analysis enhanced separation of study plots and improved environmental interpretation.

The two-dimensional RA ordination was divided into six riparian habitat regions (Fig. 1). Regions on the left included more xeric plots compared to plots on the right that had high coverage of saturated soils (Fig. 2). Region I included plots found in narrow, V-shaped and "conifer-dominated" riparian zones (Figs. 1 and 2). Typical community types (sensu Youngblood et al. 1985) within region I were *Picea/Cornus stolonifera* and *Picea/Galium triflorum*. Some narrow, patchy bands of willow communities were present on stream courses in this region. Plots in region II, "mesic meadow/conifer edge," were mesic meadow commu-

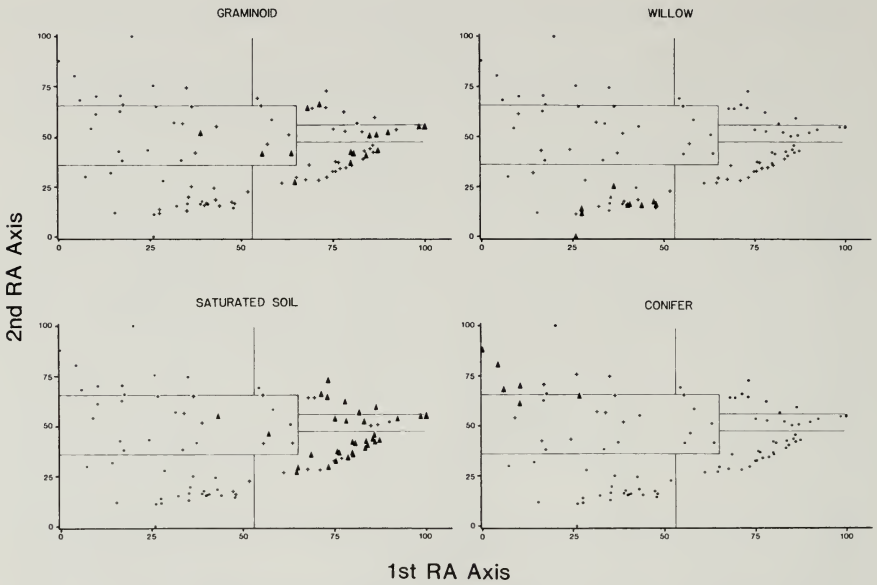

FIG. 2. Overlay of four habitat variables on the reciprocal averaging ordination of riparian zones, Centennial Mountains, Idaho, 1983 and 1984. Dots represent plots where the relative value of the variable was 0–25%, + symbols indicate plots 26–75%, and triangles indicate plots with relative values 75–100% of the largest observation recorded.

nities similar to region IV but were bordered by *Pinus contorta* communities and generally did not contain Salix spp. Plots in region III, "composite community," were heterogeneous and composed of both conifer and willow-dominated communities. These plots were typical of narrow riparian zones where willow communities were bounded by coniferous forests. Plots in region IV, "mesic meadow," were dominated by meadow communities with high graminoid coverage (Fig. 2) similar to the *Carex rostrata, C. aquatilis* and *C. nebrascensis* community types of Youngblood et al. (1985). These plots were composed primarily of *Carex* spp. and were often too wet to support woody species. Plots in regions V, "tall willow/xeric," and VI, "short willow/mesic," contained *Salix*-dominated communities (e.g., *Salix geyeriana/Carex rostrata, S. wolfii/C. aquatilis* and *S. wolfii/C. rostrata* community types of Youngblood et al. 1985). Taller, well-developed *Salix* canopies (Fig. 2) with understories of mixed grasses and forbs (e.g., *S. boothii/Smilacina stellata* community type of Youngblood et al. 1985) were found in plots of region V. Lower-stature, open-canopy *Salix* communities with *Carex* understories were found in region VI plots (Fig. 2). These habitats were common in drainages dammed and inundated by beaver.

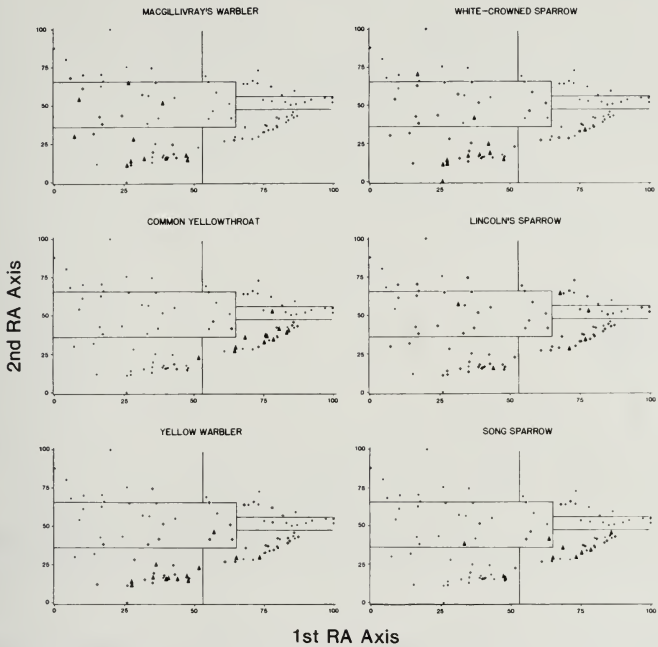

FIG. 3. Overlay of the relative frequency (percentage) of observation for six bird species on the reciprocal averaging ordination of riparian zones, Centennial Mountains, Idaho, 1983 and 1984. Dots represent plots with no observations, + symbols indicate plots with the relative frequency of observation <3%, and triangles indicate plots with a relative frequency >3%.

Separation of study sites across the second RA axis diminished as saturated soil coverage increased along the first RA axis (Fig. 2). This represented the lack of woody vegetation in the mesic meadow plots. In mesic regions, willow communities generally were low-structured and coniferous stands were decadent. As sites became more xeric, both willow and conifer communities tended to be more vigorous and productive. Thus, the contrast between willow and conifer foliage volumes was greater across the xeric portions of the moisture gradient (Fig. 2). The RA distribution of habitat variables and selected bird species may be compared by cross reference of Figs. 2 and 3.

The first habitat canonical variate was negatively correlated with saturated soil coverage, and the second variate was positively correlated with willow foliage volume. Again, an arch distortion resulted from the addition of the second axis and non-linear relationships among the variables. Interpretation was viewed across the single curved axis: a gradation from mesic meadows, into mesic short-willow communities, into xeric tall-

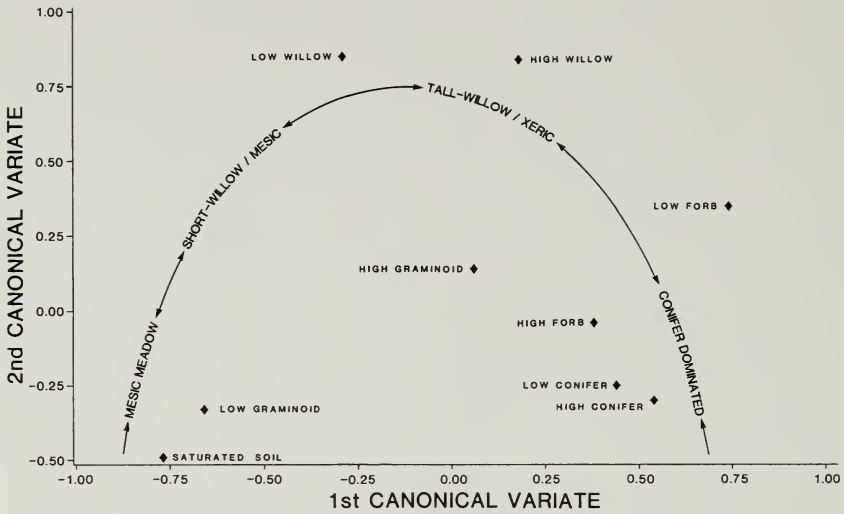

FIG. 4. Positions of the eight habitat variables on the first and second canonical correlation axes and the habitat gradient, Centennial Mountains, Idaho, 1983 and 1984.

willow communities, and finally into a conifer-dominated zone (Fig. 4). This arch, when inverted, was very similar to the RA ordination of habitat variables (Fig. 1). For similar analytical comparisons see Gauch (1982).

Avian-habitat associations.—Interdependency of the avian and habitat data sets was evident as variation in avian distributions paralleled vegetative composition along a moisture gradient. The first and second habitat variates accounted for 16% and 13%, respectively, of the standardized variance in the avian data set. The spatial arrangement of the bird species reflected their associations with the curved habitat axis (Fig. 5). The Common Snipe (*Capella gallinago*) and Red-winged Blackbird (*Agelaius phoeniceus*) were associated with wet meadow habitats. The Common Yellowthroat (*Geothlypis trichas*), Song Sparrow (*Melospiza melodia*), Tree Swallow (*Tachycineta bicolor*), and Lincoln's Sparrow (*M. lincolnii*) showed affinities with the mesic short-willow communities. The White-Crowned Sparrow (*Zonotrichia leucophrys*), MacGillivray's Warbler (*Oporornis tolmiei*), Warbling Vireo (*Vireo gilvus*), and Red-naped Sapsucker (*Sphyrapicus nuchalis*) occupied the xeric tall-willow portion of the gradient. The Willow Flycatcher (*Empidonax traillii*), Yellow Warbler (*Deudroica petechia*), and Wilson's Warbler (*Wilsonia pusilla*) were intermediate in their association with the mesic and xeric willow habitats. The Yellow-rumped Warbler (*Dendroica coronata*), Dark-eyed Junco (*Junco hyemolis*), Mountain Chickadee (*Parus gambeli*), and Western Tanager (*Pi-*

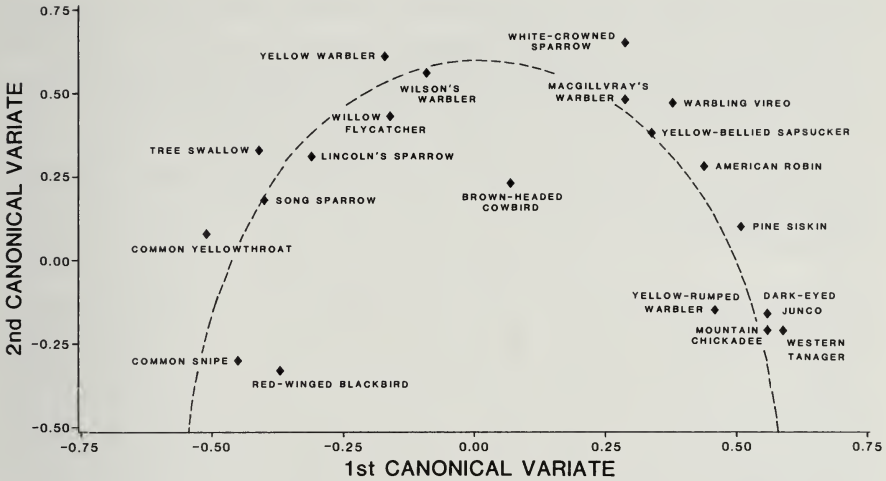

FIG. 5. Positions of 20 avian species variables on the first and second canonical correlation axis, Centennial Mountains, Idaho, 1983 and 1984.

ranga ludoviciana) were associated with the conifer-dominated areas, and the American Robin (*Turdus migratorius*) and Pine Siskin (*Carduelis pinus*) were intermediate with respect to their association with conifer and tall-willow habitats. The Brown-headed Cowbird (*Molothrus ater*) was not correlated with either axis and was centrally positioned, indicating a non-discriminating distribution.

Common Yellowthroats were observed in mesic habitats that supported low-structured willow and dense graminoid understories (Fig. 3). This species' specificity with mesic, short-willow communities (85.2% and 87.5% of 169 observations, Tables 1 and 2, respectively) resulted in its very low index of habitat breadth (Table 1). Common Yellowthroat observations were rare outside the short-willow-mesic habitat.

In contrast, the MacGillivray's Warbler occurred in xeric willow communities, primarily tall willows with mixed graminoid and forbs (Fig. 3, Table 1). Willow-conifer composite habitats (Region III) also were used by MacGillivray's Warbler, again across the more xeric portions. Compared to other species, the MacGillivray's Warbler was a specialist with respect to use of riparian habitat (i.e., willows, Table 2), which is also reflected by the low habitat breadth value (Table 1).

The Yellow Warbler displayed a general use of willow-dominated habitats (Fig. 3). Observations extended across the moisture gradient from xeric tall-willow communities into mesic short-willow habitat (Table 1). Yellow Warblers were associated with composite communities near the

TABLE 2

PERCENTAGE OF BIRD OBSERVATIONS ACROSS NINE RIPARIAN HABITAT COMPONENTS DURING THE SUMMER OF 1983–1984, CENTENNIAL MOUNTAINS, IDAHO

Species (N)	Habitat components[a]								
	Cf	As	Sn	Wl	DM	MM	Bg	Wa	Fl
Common Snipe (89)	1.1	0	7.9	12.4	1.1	0	58.4	1.1	18.0
Red-naped Sapsucker (46)	13.0	15.2	26.1	32.7	0	0	0	0	13.0
Willow Flycatcher (65)	6.2	6.1	12.3	66.1	0	0	0	0	9.3
Tree Swallow (655)	0	1.1	5.9	0.6	0	0	0.7	0	91.7
Mountain Chickadee (84)	76.2	3.6	16.7	0	0	0	0	0	3.5
American Robin (237)	14.3	8.0	39.4	7.6	0	4.7	2.5	1.7	21.8
Warbling Vireo (104)	18.3	29.8	6.7	34.6	0	0	0	0	10.6
Yellow Warbler (436)	8.7	5.3	13.8	60.1	0	0	0	0	11.7
Yellow-rumped Warbler (105)	60.0	1.9	14.3	12.4	0	0	0	0	11.4
MacGillivray's Warbler (71)	9.8	2.8	4.2	73.3	0	0	0	0	8.5
Common Yellowthroat (169)	0	0	2.4	87.5	0	0	0	0	10.1
Wilson's Warbler (109)	6.4	0	5.5	79.9	0	0	0	0	8.2
Western Tanager (66)	59.2	3.0	22.7	4.6	0	0	1.5	0	9.0
Song Sparrow (116)	5.9	0	13.9	71.6	0	0	0.9	2.6	5.1
Lincoln's Sparrow (496)	12.5	1.2	14.9	55.9	0	1.8	1.8	0.6	10.9
White-crowned Sparrow (227)	16.4	6.2	15.9	53.7	0.9	1.3	0	0	5.6
Dark-eyed Junco (152)	43.4	0.7	25.6	5.9	0	3.3	3.3	2.0	15.8
Red-winged Blackbird (329)	6.1	0	37.0	16.2	0	0	25.2	0.6	14.9
Brown-headed Cowbird (90)	15.5	3.3	67.8	11.2	0	0	0	0	2.2
Pine Siskin (462)	30.7	9.2	36.2	5.4	0	3.5	1.4	0.4	13.2

[a] Cf = conifer, As = aspen, Sn = snag, Wl = willow, DM = dry meadow, Bg = bog, Wa = water, and Fl = flight.

peripheries of willow-dominated habitats, as well as with snags and conifers adjacent to wet meadows (Regions II and IV, Tables 1 and 2). Compared to the previous two species, the Yellow Warbler had a greater habitat breadth (Table 1) and greater diversity of associated environmental components (Tables 1 and 2).

Song, White-crowned, and Lincoln's sparrows had habitat associations similar to the warbler species. The Song Sparrow exploited primarily mesic short-willow communities (Fig. 3, Table 1) and was observed most

commonly in willows (Table 2). The White-crowned Sparrow was generally observed in xeric habitats, predominantly tall willow, but also composite communities (Fig. 3, Table 1). White-crowned Sparrow use of conifer, quaking aspen, and snags was more extensive than that of the Song Sparrow (Table 2). Lincoln's Sparrows were the most widely distributed species among study plots. The very generalized distribution across riparian habitats (Fig. 3, Table 1) for Lincoln's Sparrow corresponded with a high index of habitat breadth (Table 1) and a high diversity of use of environmental components (Table 2).

Between-year variation.—Eight of the 10 analyses of variance indicated significant ($P < 0.05$) observer variability during the 1983 season. Thus, between-year variations in avian habitat use were compared with data collected by the observer common to both field seasons. Balanced sampling intensity by the common observer across years occurred at 81 plots (2 censuses/plot/year), so subsequent analyses were restricted to data collected at those plots. Wilson's Warbler was the only species that showed significant changes in distribution between years. This warbler used nine plots in 1983 that were not used during 1984. Conversely, only one plot was unique to the 1984 season. The McNemar test indicated a decrease ($P < 0.05$) from 1983 to 1984 in the number of sites used by Wilson's Warbler. This species did not display a shift in the type of riparian habitat used, but rather its range of distribution in 1984 was more restricted.

The hypothesis that study plots used in 1983 had zero similarity with those used in 1984 was not rejected ($P > 0.05$) for the Brown-headed Cowbird, Red-naped Sapsucker, Western Tanager, and Yellow-rumped Warbler. The Brown-headed Cowbird again displayed nonspecificity and was the only species observed at completely different study plots between years. Brown-headed Cowbird observations were scattered across habitat regions in 1983, but confined more to willow-dominated areas in 1984. The Red-naped Sapsucker, Western Tanager, and Yellow-rumped Warbler were observed at more sites in 1984, and all three species showed greater use of xeric tall-willow communities during the year.

DISCUSSION

Avian-habitat associations were influenced primarily by vegetative composition which was influenced primarily by soil moisture. Swift et al. (1984) reported that surface hydrology was a dominant factor affecting the plant and animal community in a Massachusetts wetland forest. In an Ozark Mountain watershed, avian distribution was correlated with vegetation physiognomy that paralleled a moisture gradient (Smith 1977). In both our RA and CCA analyses, the relationship between soil moisture and vegetation was reflected in the first habitat axis. Although this axis

portrayed a moisture gradient, it also incorporated the interdependencies between soil moisture and vegetative composition that are inherent in the analysis.

Many of the riparian bird species had discrete patterns of distribution along the moisture gradient. Such "displacement patterns" across resource axes may provide evidence that competition influences bird community composition (Cody 1974). The Song Sparrow used short-willow communities growing on mesic soils, while the closely related White-crowned Sparrow exploited xeric, tall-willow habitats (Table 1). The Common Yellowthroat occurred in short-willows, and the MacGillivray's Warbler used tall-willows (Table 1). These non-overlapping ranges afford ecological isolation through habitat segregation.

Cody's (1974) investigation of avian distribution in willow habitats near Jackson Hole, Wyoming, included several species common to this study. He reported that territories of Song Sparrows, Lincoln's Sparrows, and Common Yellowthroats occurred in low-structured willow vegetation and that those of MacGillivray's Warblers and White-crowned Sparrows occurred in patches of tall willow. The structural aspects of Yellow Warbler territories were intermediate between those of the Common Yellowthroat and MacGillivray's Warbler. Our results are consistent with Cody's findings, as well as displaying the relationship between soil moisture and vegetative composition. The Brown-headed Cowbird was not correlated with either CCA axis. Its central position in Fig. 5 indicates an indiscriminating distribution with respect to the habitat gradients. Brown-headed Cowbirds are brood parasites and have been reported to lay eggs in the nests of 214 species (Friedmann 1971). Their nonspecific distribution in the riparian habitat may represent a relatively general search for host species nests and/or broad habitat tolerance.

Extending the RA analysis into two dimensions improved interpretations of avian-habitat associations. Species overlapping along one resource axis may have clear ecological separation if additional axes are considered (Pianka et al. 1979). The Yellow Warbler had a broad distribution across the first RA axis. The second RA axis revealed its use of willow-dominated communities, thereby distinguishing it from species associated with coniferous habitats.

The second RA axis contrasted vegetative characteristics of the riparian region (conifer vs willow dominance). Both vegetative structure and species composition, which are not independent variables, are reported to influence avian habitat use (Rice et al. 1984). This study used structural aspects of the habitat by measuring foliage volumes of each lifeform (conifer, willow, forb, graminoid) at various strata. Although structural aspects alone (especially the vertical profile) correlate with avian distri-

bution in many habitats (MacArthur and MacArthur 1961, MacArthur et al. 1966, Anderson and Shugart 1974, Erdelen 1984), distinguishing structure with respect to lifeform improved the resolution of avian-habitat associations without adding excessive variables into the multivariate analyses (Johnson 1981b).

The RA and CCA analyses produced very similar structuring of the riparian habitat. This was interesting because RA constructed the habitat axes based on habitat data only, but CCA derived habitat axes under the constraint that they were maximally correlated with avian abundance. Both analyses supported the relationship between the avian distribution and the primary gradients within the riparian habitat.

Analyses of between-year variations in avian distributions considered variation due to observers (Faanes and Bystrak 1981) and to sampling intensities (Scott and Ramsey 1981). The 1983 data were collected during an "early season" period (8 June to 21 July), while in 1984 the censusing was during a "late season" period (5 July to 2 September). These sampling differences were unavoidable due to changes in spring snow cover between years. For several bird species, studies have shown that habitat use varies across seasons (Rice et al. 1983, Anderson and Ohmart 1983, Anderson and Ohmart 1985, Hutto 1985) and that detection may also change (Best 1981). Thus, the more extensive exploitation of tall-willow/xeric habitats in 1984 by the Western Tanager, Red-naped Sapsucker, and Yellow-rumped Warbler may be due to seasonal shifts in habitat use and/or sampling detection.

Although riparian zones are often considered a single discrete type of wildlife habitat (Thomas et al. 1979), our data indicate that there are distinct regions within the riparian zone with characteristic avian species use. If the relative position of a site along a habitat gradient were changed, the avian species using that site would be expected to change. Altering the dispersion of water within a riparian zone may be the most dramatic management practice affecting future plant and animal communities. Construction of dams and holding ponds, stream channelization, altering stream courses, and introduction or control of beaver populations are examples of environmental changes that alter soil moisture and, consequently, the avian community. Similarly, conifer, willow, or other lifeform dominance can be altered by vegetative changes associated with timber harvest, grazing, or fire.

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COLONIAL WATERBIRD POPULATIONS IN THE SIAN KA'AN BIOSPHERE RESERVE (QUINTANA ROO, MEXICO)

ARTURO LOPEZ-ORNAT[1] AND CRISTINA RAMO[1]

ABSTRACT.—This is the first colonial waterbird survey in the Sian Ka'an Biosphere Reserve, the largest wetland ecosystem (ca 350,000 ha) in the Yucatán peninsula. We counted birds at breeding sites and feeding concentrations during aerial and boat surveys in seasons between 1982 and 1988. An annual mean of 1259 pairs of three species of Pelecaniformes and 3118 pairs of nine species of colonial Ciconiiformes were found breeding at 15 locations in the study area. Seasonal variations of the Ciconiiform populations were found to follow the changes in the water levels. For some of the breeding species, populations in the study area were found to be of regional and national importance to the Atlantic and Pacific coasts of Mexico. *Received 27 June 1991, accepted 26 Jan. 1992.*

Wetlands in Mexico have received little attention from ornithologists, although they are known to harbor important populations of waterbirds (Sprunt and Knoder 1980, Saunders and Saunders 1981, Scott and Carbonell 1986). Some of the most extensive coastal wetlands in North and Central America and the Caribbean occur in southeastern Mexico, namely in the Usumacinta-Grijalva Delta on the gulf coast, and in the limestone wetlands that almost entirely surround the flat Yucatán peninsula. This wetland belt around the peninsula has a varying width, up to 25–35 km inland in the central coast of Quintana Roo where the Sian Ka'an reserve lies.

Coastal wetlands in Mexico were periodically censused for wintering ducks and geese, from 1937 to 1964, by the U.S. Fish and Wildlife Service (Saunders and Saunders 1981), but few references were made to Ciconiiformes. Although these birds share their habitat with the waterfowl, their populations do not concentrate at the same time of the year. Other information on colonial waterbirds in southeastern Mexico are from annual aerial censuses carried out from 1971 to 1980 (Sprunt and Knoder 1980, Ogden 1987) on the gulf coast and in the western and northern coasts of the Yucatán peninsula. None of these workers, however, surveyed the Caribbean coastal wetlands in detail due to their great size, limestone ecology with low productivity, and apparently unimportant populations of waterfowl (Saunders and Saunders 1981) and colonial waterbirds (Sprunt and Knoder 1980). Only the Greater Flamingo (*Phoenicopterus ruber*)

[1] Estación Biológica Doñana, Av. Ma. Luisa s/n. Sevilla, 41013, Spain.

breeding colony in the northern coast of the Yucatán State has been studied in some detail (Espino-Barros and Baldassarre 1989).

Together with the establishment of a large protected area in Quintana Roo, flights and field trips were carried out on these almost unknown wetland systems, and important populations of breeding Ciconiiformes and Pelecaniformes were found. The results of periodic visits to the main breeding colonies and feeding grounds in 1982 through 1988 are presented in this paper. The importance of these populations at regional and national levels is discussed.

STUDY AREA

The study area is the Sian Ka'an Biosphere Reserve in the eastern coast of the Yucatán peninsula (state of Quintana Roo) (Fig. 1). The reserve includes 178,000 ha of coastal marshes, mangroves, inland savannas, 20,000 ha of freshwater lagoons, 180,000 ha brackish coastal lagoons, and two broad shallow bays, Ascensión and Espíritu Santo.

The weather is classified as "Savanna" by García (1964); mean annual precipitation (between 1961 and 1980) was 1150 mm, most of it (72.4%) between June and October. Seasonal flooding affects most of the reserve's surface. Water varies from fresh to marine, depending on distance to the coast and the precipitation input at each different time of the year. The vegetation varies accordingly. Wetlands are covered with grasses such as *Phragmites australis, Typha angustifolia* and especially *Cladium jamaicense* (sawgrass) together with some emergent savanna trees. A description of the vegetation types in the reserve is found in Olmsted et al. (1983).

Eleven hurricanes have hit the coast of Sian Ka'an since 1900 (Jauregui et al. 1980), periodically flooding parts of these lowlands with salt water. In depressed areas, salinity can be high even far from the coast, and they are covered by dwarf red mangrove (*Rhizophora mangle*). These important areas for waterbirds (62,000 ha) are the only remaining surface water during most of the dry season when *Cladium* marshes are dry (Lopez-Ornat 1983a). red mangrove trees, 6 to 10 m high, form a forested fringe around the coastline; mangrove trees of *Rhizophora* and *Avicennia* also cover the numerous small islands emerging from the bays and the coastal lagoons and are the favorite breeding sites for the colonial waterbirds.

METHODS

Wading birds were counted during all months, from 1982 to 1986, both at their breeding sites and dry season feeding concentrations. Pelecaniformes were counted only at breeding aggregations. Counts were made from fixed-wing aircraft and by boat. Breeding colonies, when possible, were photographed from aircraft from a height of 100 m. Ground surveys were then made by boat to identify species and to count the breeding pairs of those species nesting under the canopy. Transect flights were also made during the wet season (non-breeding) and during the dry season to locate feeding concentrations and seasonal changes in habitat use. Each linear transect on the Sian Ka'an wetlands is around 100 km long. We also made flights on the following dates: in 1982, 20 March, 12 July, and 2 December; in 1983, 16 February, 4 May, 30 June, 6 September, and 7 October; in 1984, 9 February and 14 April; in 1985, 4 March and 20 May. All flights were from 07:30 to 09:00, flying at 160 km/h and 100–150 m altitude on fixed transects over the coastal marshes and keys. Additionally, two flights on 11 and 26 April 1986 covered almost the entire wetland surface of the reserve, in search of other previously unknown colonies.

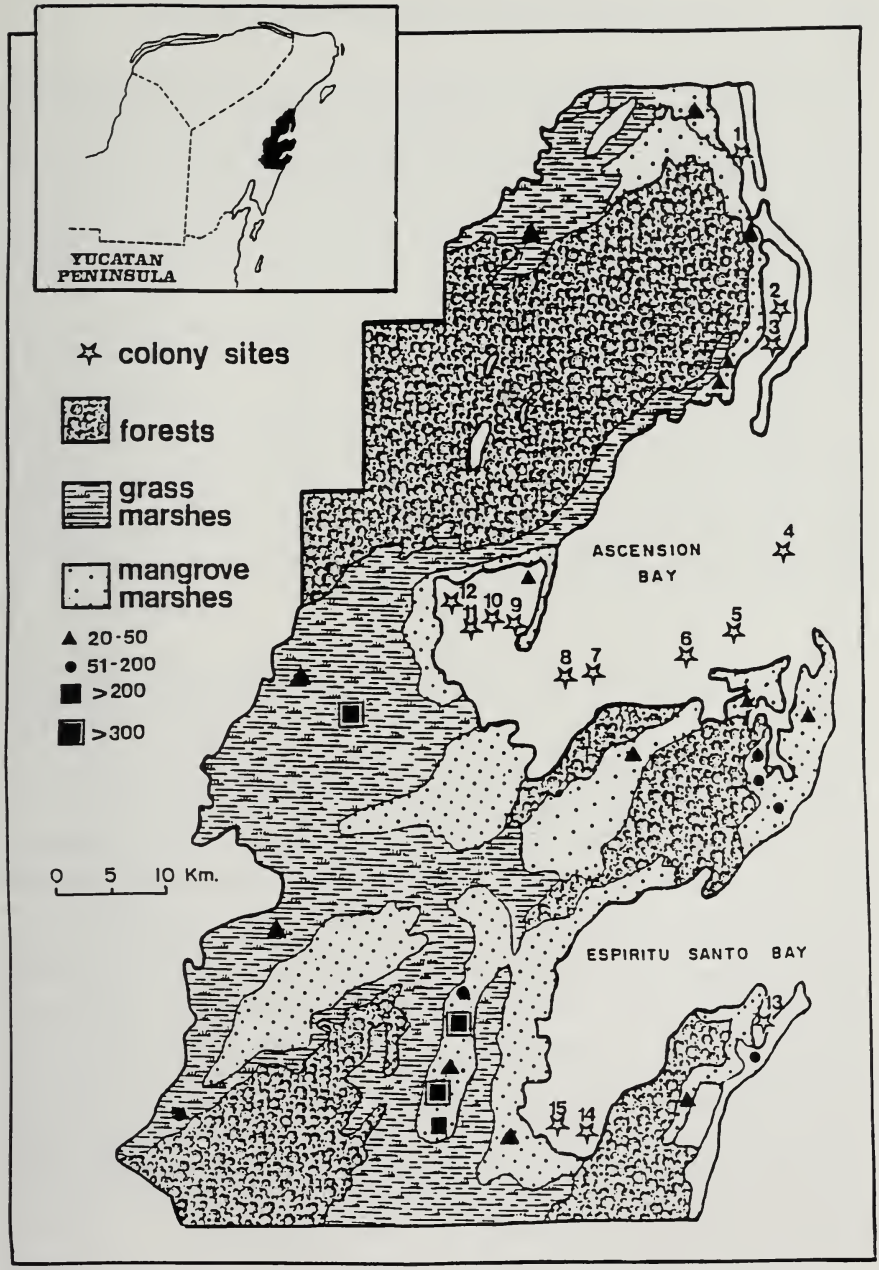

FIG. 1. Map of the Sian Ka'an Biosphere Reserve with vegetation types and locations of colonies and feeding concentrations. Data on concentrations of fewer than 200 individuals are from April 1986. Concentrations higher than 300 individuals are from May 1983.

A small boat, pushed by a pole to prevent noise, was used to check breeding colonies. We entered a colony only when accurate estimates or identification were otherwise impossible. In small colonies, all the active nests were counted. In those with more than ca 100 pairs, the number of adults was estimated by counting all active nests in two 100 m^2 plots (10 × 10 m) and extrapolating densities to the estimated surface of the key occupied by each species. Canopy nests were checked with a mirror attached to the end of a 6-m extensible aluminum pole. Boat trips around Ascensión Bay (localities 1 to 12 in Fig. 1) took place on the following dates: 1982, 22 May, 26 August, and 28 November; 1983, 30 January and 5 June; 1984, 10 April, 15 May, and 24 June; 24 April 1985, 7 June 1987, and 22 April 1988 plus once every 15 days throughout the breeding season (January to July) of 1986. Due to logistic difficulties, localities 13, 14, and 15 were visited only on 4 June 1983, 11 May 1984, and 22 March and 22 May 1986.

To determine the regional importance of the breeding populations in the reserve, we surveyed information available for colonial waterbirds in Mexico, which is detailed only for some areas. For the Pacific coast, we found only local surveys (Vargas 1976, Voelzer et al. 1980, Alvarez del Toro 1980). More information was found for the gulf coast (Sprunt and Knoder 1980, Blankinship 1986, Correa 1987, Ogden 1987) and for the Yucatán peninsula (Brazda et al. 1980, Rogel Baena 1980, Sprunt and Knoder 1980, Blankinship 1986, Espino-Barros and Baldassarre 1989). The Neotropical wetland survey of Scott and Carbonell (1986) provided some complementary information.

RESULTS

Nesting populations.—We regularly encountered six species of Pelecaniformes and 20 species of Ciconiiformes in the study area and 12 total species in breeding colonies. Fifteen breeding colonies were located in the reserve (Fig. 1), nine of which held more than 100 pairs. All colonies were on small islands at distances of 0.5–12 km from the coast.

An estimated mean of 1259 pairs of three species of Pelecaniformes and 3118 pairs of nine species of colonial Ciconiiformes bred in the study area (Table 1). The Magnificent Frigatebird (*Fregata magnificens*) accounted for 70% of pelecaniform nests; the White Ibis (*Eudocimus albus*) and the Woodstork (*Mycteria americana*) accounted for 41% and 23% of all ciconiiforme nests, respectively. Inter-year variations in the number of nests censused for each species in five years were small (Table 1), the standard deviation being of 17% of the mean in Ciconiiformes and 27% in Pelecaniformes. Table 2 shows the number of active nests for each colony and colonial species in the intensive counts during 1986. In 1987 and 1988, the number of breeding Pelecaniformes remained at about 80% of the 1982–1986 mean, while the breeding Ciconiiformes (1988) dropped to 25% of the previous five-year mean (see Discussion).

Only the Magnificent Frigatebird concentrated its nests every year at the same key. Other species used 2–10 different breeding sites each year (Table 3). Some species of colonial wading birds seemed to have a single "preferred" breeding colony, which accounts for about 50% of all nests in any given year. The exceptions to this trend were the Roseate Spoonbill

TABLE 1
NUMBER OF ACTIVE NESTS OF COLONIAL WATERBIRDS IN SIAN KA'AN

Species	1982[a]	1983	1984	1985	1986	1982–1986[b]	1987[a]	1988[a]
Pelecanus occidentalis	25	85	58	32	35	47 ± 24	30	37
Fregata magnificens	700	1000	1130	1000	550	876 ± 241	600	700
Phalacrocorax olivaceus	202	456	416	325	284	336 ± 101	300	267
All Pelecaniformes	927	1541	1604	1357	869	1259 ± 343	930	1004
Ardea herodias	ND[c]	ND	ND	ND	36	—	ND	ND
Casmerodius albus	ND	360	430	ND	437	409 ± 42	ND	45
Egretta thula	ND	162	140	ND	168	157 ± 15	ND	25
E. rufescens	ND	41	48	ND	51	47 ± 5	ND	35
E. tricolor	ND	285	253	ND	226	254 ± 29	ND	36
Cochlearius cochlearius	ND	32	27	36	27	30 ± 4	ND	16
Eudocimus albus	900	1120	1660	895	1465	1208 ± 343	ND	550
Ajaia ajaja	162	150	138	144	182	155 ± 17	ND	110
Mycteria americana	765	740	630	700	548	676 ± 88	ND	33
All Ciconiiformes	—	2890	3326	—	3140	3118 ± 218	—	850
Total pairs	—	4431	4930	—	4009	4456 ± 461	—	1854

[a] Keys 13, 14, and 15 not censused.
[b] Mean ± SD.
[c] ND = birds not censused.

(*Ajaia ajaja*), Great Egret (*Casmerodius albus*), and Snowy Egret (*Egretta thula*), which distributed their nests fairly regularly among 7–10 colonies every year. White Ibis (*Eudocimus albus*) moved from its favorite site after the irregular precipitation of 1986.

Seasonal variations.—Flight counts showed a clear seasonal pattern for the Ciconiiformes. Most of these species were absent from the study area in summer (mid-June to late-September; Fig. 2), while numbers peaked between February and May. Feeding concentrations occurred where water bodies had receded. The first groups (5–20 individuals) were found in inland marshes of sawgrass and *Typha* as water receded in January. The size of these aggregations grew (5–200) in February and March as the dry season progressed. In March and April, feeding groups (20–150 individuals) were frequently found in the mangrove scrub, as this formation dries later than the sawgrass marsh. In May, when chick feeding should be at its highest demand, the peak of the dry season had dried out most of the "dense" mangrove scrub; the last flooded grounds remained in the "scattered" mangrove scrub, where the highest concentrations of wading birds (250–600 individuals) were found at this time of the year (Fig. 1). When the rains began in late May or in June, the wetlands were gradually reflooded. By mid June, all the birds had completed their breeding, and

TABLE 2

NUMBER OF ACTIVE NESTS FOR EACH COLONY AND COLONIAL SPECIES IN THE INTENSIVE COUNTS OF 1986 AT SIAN KA'AN

Species	Colonies														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Pelecanus occidentalis	26	—	—	9	—	—	—	—	—	—	—	—	—	—	—
Phalacrocorax olivaceus	83	—	—	68	100	—	6	7	—	—	—	—	20	—	—
Anhinga anhinga	—	—	—	—	—	—	—	—	—	?	—	—	—	—	—
Fregata magnificens	—	—	—	550	—	—	—	—	—	—	—	—	—	—	—
Ardea herodias	2	2	—	—	30	—	—	1	—	—	—	—	1	—	—
Casmerodius albus	48	—	—	—	1	5	—	50	—	55	11	—	46	80	141
Egreta thula	50	13	—	—	20	1	—	15	—	50	?	—	19	—	—
E. rufescens	2	6	—	—	—	34	—	7	—	?	?	—	2	—	?
E. tricolor	6	16	20	—	100	20	—	26	—	?	—	—	38	—	—
Cochlearius cochlearius	12	3	—	—	4	2	—	—	—	?	—	—	6	—	?
Mycteria americana	—	—	—	—	—	—	—	—	—	376	100	53	—	—	19
Eudocimus albus	—	—	150	—	1255	—	—	—	—	60	—	—	—	—	—
Ajaia ajaja	13	8	—	—	34	20	—	58	14	10	6	—	7	—	12

TABLE 3

EXTREME DATES FOR EGG OBSERVATIONS, TOTAL NUMBER OF BREEDING COLONIES, LOCATION OF THE MAIN COLONIES (SEE FIG. 1), AND ESTIMATED RELATIVE IMPORTANCE OF THE SIAN KA'AN BREEDING POPULATIONS IN ALL OF THE MEXICAN ATLANTIC COAST AND IN ALL OF MEXICO

	Number of breeding colonies	Main colonies at keys num.	Extreme dates for egg observations	Percent population of	
				Atlantic Coast	All México
Phalacrocorax auritus	6	4, 5	18 Jan.–24 Aug.	ND	ND
Fregata magnificens	1	4	11 Nov.–4 May	10–12	ND
Pelecanus occidentalis	5	4	17 Jan.–21 May	20	15
Ardea h. occidentalis	3	1, 5	3 Dec.–5 May	100?	100?
Casmerodius albus	8	14, 15	3 March–14 Apr.	2	ND
Egretta thula	8	1, 10	3 Apr.–18 May	2	ND
E. rufescens	8	6	3 Dec.–6 June	25	15
E. tricolor	8	5	2 March–23 June	5	ND
Cochlearius cochlearius	6	1	5 Jan.–15 Apr.	ND	ND
Jabiru mycteria	—	—	13 Jan.–18 Feb.	20	20
Mycteria americana	4	9, 10	25 Feb.–19 Apr.	5	5
Eudocimus albus	4	8	3 Apr.–7 June	20	20
Ajaia ajaja	10	8, 15	18 Jan.–18 Apr.	20	10

both adults and immatures soon left the reserve. From July to October, only scattered Ciconiiformes were found, accounting for 0–10% of the populations censused during the breeding season (Fig. 2). Immature Wood Storks, White Ibises, and Roseate Spoonbills were found in small roosts in open fields far from the coast in summer.

Breeding species accounts: status, seasonality and regional importance of populations.—The timing, location, and size of breeding of Sian Ka'an colonial breeders is shown in Table 3 and the following species accounts:

Olivaceus Cormorant (*Phalacrocorax olivaceus*).—Nests were located at least on six keys, sometimes scattered along the mangrove fringes. There are no surveys on this species for the Atlantic coasts of Mexico.

Magnificent Frigatebird.—Extreme dates for males observed with extended red pouch are 14 October and 4 May. Feathered young were still in the nests by late October. Frigatebirds were seen scavenging over other colonies where Ciconiiformes bred (see Gibbs and Gibbs 1987, Mora 1989). In Mexico, 500–1000 pairs are reported for the mid and south Pacific coast (Scott and Carbonell 1986) and ca 3000 pairs for the Atlantic coast, all of them at small islands around the Yucatán peninsula (Rogel Baena 1980, Sprunt and Knoder 1980). The Sian Ka'an population would then harbor at least 20% of all the Atlantic coast population.

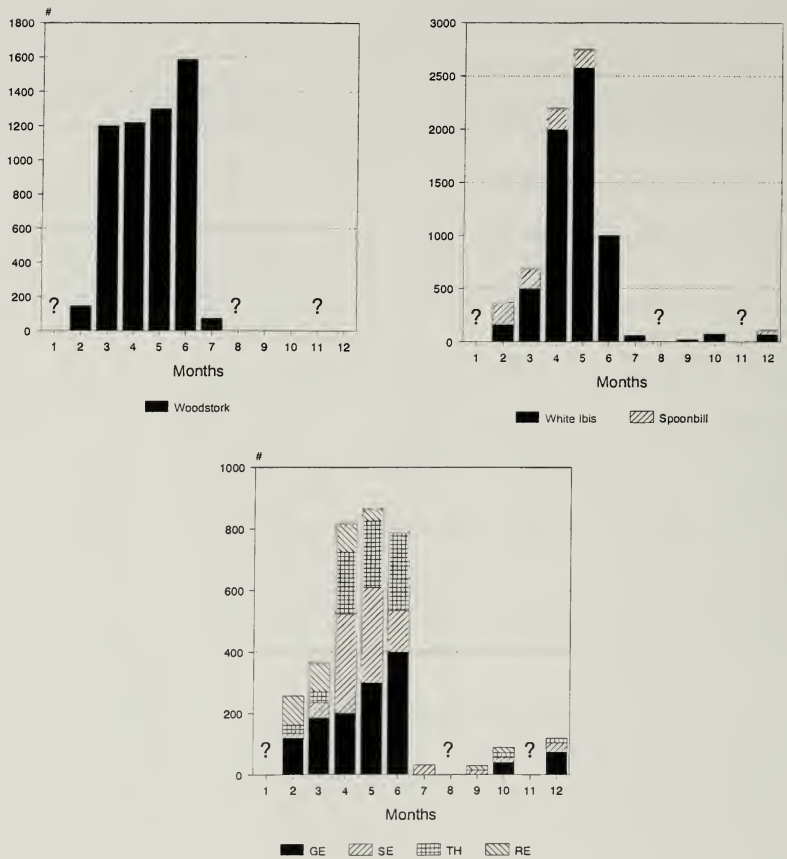

FIG. 2. Indicators of seasonal variations in the number of individuals of seven Ciconiiform species in Sian Ka'an. Combined data of 1983 thru 1986 aerial censuses. (RE = Reddish Egret; TH = Tricolored Heron; SE = Snowy Egret; GE = Great Egret.) Months of January, August, and November were not censused by aircraft in any year. Months from February through June were censused more than once.

Brown Pelican (*Pelecanus occidentalis*).—Brown Pelicans have recovered in their Texas breeding grounds from 10 nesting pairs in the early 1970s to 300 nesting pairs in 1986. In Mexico, however, a contrary trend brought down the population of breeding pairs in the Atlantic coasts from 910 in 1980 to 428 in 1986, the possible causes being human disturbance, ticks and disease, and chemical pollution (Blankinship 1986). The Sian Ka'an breeding population would then be 10–12% of that in all the Mexican Atlantic coasts.

Great Blue Heron (*Ardea herodias*).—The feeding population dropped

to about one third in summer. In Sian Ka'an, this species presents three different color phases which are considered to belong to the same species (Meyerriecks 1957). The white phase (*A. h. occidentalis*) in Florida favors marine environments as compared to the dark one (Mayr 1956, Meyerriecks 1957), and so does the intermediate morph (*A. h. würdemanni*). In Sian Ka'an, coastal-marsh boat surveys reveal that 65% of the Great Blue Herons are dark, 25% intermediate and 10% white, while in marine environments (outer keys), white birds constitute 50% and dark birds 30% of all the individuals counted. Monitoring over 13 nests of the species in 1986, containing one to three young each, revealed that eight nests had dark young, 4 had only white young and one nest in key 5 had one dark and one white young. The highest density of *A. h. occidentalis* is found in Florida Bay (Robertson and Kushlan 1974) (2500 individuals), where populations seemed stable (Ogden 1978), although reproductive success has recently declined (Powell et al. 1989). The species is also present in small numbers in some Caribbean islands (Meyer de Schauensee and Phelps 1978). The five nests reported here are the first known in Mexico for this subspecies.

Great Egret.—Roosts of up to 200 birds were found in July, away from the breeding grounds. Scattered individuals (ca 10–25% of total breeding population) could still be found in inland marshes during the rainy season (July to October). By late October, Great Egrets started coming back into the area, and by December they formed the first important feeding concentrations in the inland marshes.

Snowy Egret.—Postbreeding dispersal in July, and other patterns in the repopulation of the area during the fall, were similar to those of the Great Egret. Based on current literature, the Sian Ka'an populations of these two species would represent only 2% of the population of Mexico. Both Snowy and Great egrets have their main populations in the Usumacinta Delta.

Reddish Egret (*Egretta rufescens*).—Both known color phases were present. Seventeen nests monitored in 1986 (1 to 3 chicks each) had 24 dark and 11 white chicks. Two of these nests had one dark chick and one or two white ones at a time. The species was almost absent during the summer. In the United States, this species was close to extinction due to feather collectors in the early part of this century and to high pesticide concentration in the mid century (Paul 1977), but populations were stable around 2000 pairs thereafter (Portnoy 1978, Ogden 1978). The whole Mexican population is estimated at 300–400 pairs. Sian Ka'an harbors 15–20% of these, second in importance only to the Holbox coast (about 130 pairs) in northern Q. Roo and the Mar Muerto in Chiapas (about 70 pairs) according to Alvarez del Toro (1980).

Tricolored Heron (*Egretta tricolor*).—Around 20% of the individuals remained in the area during the summer, especially in salt water.

Wood Stork.—The first adults were seen in early November, and numbers grew until breeding activities started around mid-February. It bred only on the most secluded keys. The number of pairs showed small annual variations, with extremes of 550 and 765 active nests per year. All birds left the area in mid-June, although in dry years, small groups were found feeding until mid-July. All chicks died in 1986, due to a premature and heavy rainfall in May, which flooded all habitats, dispersing the prey (Ramo and Busto, unpubl. data). Only 33 nests were counted in 1988. This is an endangered species in the United States (U.S. Fish and Wildlife Service 1984), very sensitive to habitat destruction and water drainage (Kushlan 1981, Frederick and Collopy 1989). 12,000 pairs of this species breed in Mexico, 65% of them in the Usumacinta Delta region (Ogden 1987), which by far constitutes the greatest concentration in Central and North America. Sian Ka'an is the next area in importance for this species in the Atlantic coasts of Mexico.

White Ibis.—The White Ibis was the most abundant colonial waterbird in the reserve. In different years, 900 to 1600 nests were active from April to June. Key 5 contained 80% of the nests. An estimated 10% of these birds stayed in the area during the summer; other than this, their seasonal pattern was similar to that of the Wood Stork. After the 1986 chick mortality, the main colony in key 5 was deserted during the 1987 and 1988 breeding seasons. In 1987, only 150 nests were found (key 6) and in 1988, 500 pairs were again breeding, mostly in the keys previously occupied by Wood Storks (10 and 11). Around 9000 pairs of the White Ibis have been censused in Mexico, roughly half of them in the Usumacinta Delta region. Our study area is the second area in importance for this species in the country.

Roseate Spoonbill.—Between January and May, active nests were found in small numbers at almost every colony. Almost no birds were found from June to September, and in October groups of 5–10 roost or feed with other Ciconiiformes in the mangrove scrubs and shallow coasts. Greater aggregations (15–30 and up to 60) were found from November on. After the breeding depression in 1986, no apparent negative impact was noticed in the species' breeding numbers. Along the coasts of Mexico, 4000 individuals of this distinctive species have been surveyed, one third at the Usumacinta Delta region, and another third in the Pacific coasts of Nayarit. About 10% have been found breeding at Sian Ka'an.

Other species.—Groups of up to 150 Greater Flamingos (*Phoenicopterus ruber*) were found every winter (extreme dates 7 October and 22 May) in areas located close to keys 1, 9 and 14. They breed in April–August at

Rio Lagartos in the northern Yucatán coast, ca 400 km away from the Sian Ka'an wintering grounds.

Only a few pairs of Anhingas (*Anhinga anhinga*) have been found in inland water bodies. The Brown Booby (*Sula leucogaster*) was also scarce; only four to 12 immatures were found every year in key 4 between April and August; Double-crested Cormorant (*Phalacrocorax auritus*) was seen in small numbers (3 to 7) in February and March.

Yellow-crowned Night-Herons (*Nycticorax violaceus*) and Black-crowned Night-Herons (*N. nycticorax*) probably also breed in small numbers in mixed heronries in Sian Ka'an, as immatures and adults were seen in several mangrove stands.

Cattle Egrets (*Bubulcus ibis*) were found inland at cattle ranches and dumps. We have not found any nests in Sian Ka'an. Noteworthy migratory movements were registered northwards in April–May and southwards in October; the birds flew close to the coast in groups of 30–200, adding up to more than 1000 birds most of the days. Extreme dates for northward movements in Puerto Morelos were 12 April and 9 June, and for southward movements 27 September and 30 October. Both in April and November, we found roosts of 30–200 birds at different keys and coastal localities in Sian Ka'an.

Little Blue Herons (*Egretta caerulea*) were found in small numbers feeding with other Ardeidae at any time of the year, except in May and June when they were absent. The winter population estimate is of 100–200 birds. The average for twelve boat transects in winter months was of 75% adults and 25% immatures (86:29). Small migratory groups (3–15 individuals) followed the same routes and dates as Cattle Egrets, although in much smaller numbers and with an irregular schedule.

Two non-colonial breeding species have been observed: two Bare-throated Tiger-Heron (*Tigrisoma mexicanum*) nests with eggs in late March and one Jabiru (*Jabiru mycteria*) nest with two eggs (Lopez-Ornat et al. 1989). The latter species is noteworthy as one of the only four nests known for Mexico (Correa 1987) is found in the Sian Ka'an reserve, where up to five different individuals have been regularly seen between extreme dates of 22 November and 10 April. The Mexican lowlands constitute the Northern geographic limit for this always uncommon bird. 202 individuals were found at Los Llanos in Venezuela (Ramo and Busto 1984), only 127 individuals and 17 nests in Central America (Luthin 1984). Since 1987, this is the only wading bird species protected by law in Mexico.

Other Ciconiiformes present were Least Bittern (*Ixobrychus exilis*) and Pinnated Bittern (*Botarus pinnatus*), both apparently uncommon, and Green-backed Heron (*Butorides striatus*) a common solitary species, all three found throughout the year. Glossy Ibises (*Plegadis falcinellus*) were

found four times at two locations in groups of one to three individuals between 6 March and 24 May. No censusing of these species has been done in Mexico.

DISCUSSION

Seasonal variations.—Seasonality in the populations of Ciconiiformes follows the changes in prey availability with the receding water levels in the marshes, as was found in Florida (Kahl 1964, Kushlan et al. 1985, Frederick and Collopy 1989).

In May 1986, a very heavy early rain flooded all the lowlands of Sian Ka'an. Adult Wood Storks were forced out of the region, leaving more than 1000 feathered chicks to starve. Although these colonies could not be reached in 1987, only 33 Wood Stork pairs were counted in 1988. The negative impact of 1986's premature rains on the Ciconiiformes was severe on all species with late breeding (Wood Stork, Great Egret, Snowy Egret, and probably White Ibis); these same species were also negatively affected by early rains in Florida (Kushlan 1978a, Frederick and Collopy 1989). Early breeders like Roseate Spoonbill and Reddish Egret did not show a breeding population decrease in 1988. The latter species do not depend as strongly on inland water conditions, feeding mainly in the marine and brackish shallows. Ogden (1978) suggested that this fact has helped both species to maintain their populations in the southern Florida environments which are threatened by dessication of inland water bodies by human development.

Because the Pelecaniformes are not dependent on the flooding regimes in the marshes, they were found breeding at all times of the year; these species were apparently not affected by the 1986 anomalies. Lower breeding activity during the summer and early fall may be a consequence of the periodical occurrence of tropical storms and hurricanes at this time of the year.

Importance of the populations.—As compared to the Usumacinta Delta region, the density of Ciconiiformes breeding in Sian Ka'an is much lower. Primary productivity in limestone wetlands should be lower than in nutrient-rich deltaic ecosystems. Nevertheless, the extent and variety of wetland ecosystems in the study area allow for significant populations to breed.

The study area has both a regional and national importance for the conservation of colonial waterbirds. For a majority of the Ciconiiformes treated here, the wetlands protected in the Sian Ka'an reserve contain the most important breeding populations in the Yucatán peninsula. Within all of the Atlantic coastal wetlands of Mexico (gulf and Caribbean), the study area still harbors one-eighth to one-fourth of all the known breeding

pairs of species such as the Magnificent Frigatebird, Brown Pelican, Reddish Egret, Jabiru, White Ibis, Roseate Spoonbill, and possibly the Wood Stork, and contains all the known nests of the Great White Heron in Mexico.

Colonial waterbirds in Sian Ka'an are likely to maintain their present population levels in the long term, provided disturbances are kept as low as to date. The area is dotted by dozens of isolated keys that could be potentially used for breeding purposes; it also includes a broad array of diverse wetland systems which should provide feeding grounds in most seasonal circumstances, except perhaps when rains are premature and heavy. Natural events such as the latter take place periodically, but populations are likely to recover (Frederick and Collopy 1989) as long as the general ecological conditions do not change.

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SHORT COMMUNICATIONS

Temporal stability of song in a local population of Wood Thrushes.—In many species of songbirds, individuals acquire song through social learning (see review by Slater 1989). As a result, song is subject to cultural evolution. Inferences about the process of cultural evolution can be made from an analysis of geographical variation in song, and a number of studies has taken this approach (see, e.g., Lynch et al. 1989 and references therein). A second approach, more direct than the first but also more time-consuming, is to examine temporal changes in song within a population (e.g., Thompson 1970, Jenkins 1978, Ince et al. 1980, Payne et al. 1981, McGregor and Krebs 1982, Payne 1985, Gibbs 1990).

Here I examine temporal variation within a population of Wood Thrushes (*Hylocichla mustelina*). An earlier longitudinal study which compared samples of Wood Thrush song recorded 14 years apart in Sapsucker Woods, Ithaca, New York, revealed no significant differences between the samples (Whitney and Miller 1987a). That study, however, was based on small sample sizes, and my objective here is to present more detailed and compelling evidence for a lack of temporal change in Wood Thrush song.

Materials and methods.—I compared two samples of song recorded from Wood Thrushes living on and near the grounds of the Rockefeller University Field Research Center, Millbrook, New York (see fig. 2 of Whitney and Miller 1987a). One sample was recorded in 1981 (8 May–4 June) and the second in 1990 (6–9 June) (N = 36 and 26 birds, respectively). Copies of these recordings are available from the author.

A typical Wood Thrush song has three phrases, referred to as the A, B, and C phrases (for sonagram, see fig. 1 of Whitney and Miller 1987a). The introductory A phrase consists of one or more low-pitched sounds, the middle B phrase is of loud, flute-like notes, and the ending C phrase is usually a trill. My analysis is based on the structure of the B phrase, which is the only part of the song that appears to be learned by imitation (Lanyon 1979, Whitney and Miller 1987b). Individual males have repertoires of two to eight different B phrases.

In both years, I attempted to record a sequence of at least 30 songs from each bird. This seemed adequate to identify the complete B phrase repertoire, since Wood Thrushes typically cycle through their repertoires in sequences of 15 songs or fewer. Recordings were made with a Uher Report IC tape recorder equipped with either a Sennheiser MKH 815T directional microphone or a Dan Gibson P650 parabolic microphone and a Sony TC-D5M cassette recorder equipped with either a Dan Gibson P650 or a Sony PBR-330 parabola and Sony ECM-170 microphone.

Sonagrams were prepared with a Macintosh Plus computer, a MacADIOS 411 hardware unit, a TTE 411AFS amplifier and anti-aliasing system, and MacSpeech Lab software (GW Instruments). The recording sample rate of the system was set at 10.416 kHz (according to which rate the maximum frequency displayed on a sonagram is 5 kHz), and the wide band filter (300 Hz) was used. I measured durations of song parameters from wide band sonagrams and dominant frequencies from narrow band (45 Hz filter) "spectrum" waveforms.

Results.—The system of song classification used in this study was described in detail in an earlier paper (Whitney and Miller 1987a) and is based on the 1981 sample. It placed 141 of the 154 songs (92%) in that sample into 25 discrete structural types (Table 1). Applied to the 1990 sample, the system classified 105 of 114 songs (92%). Twenty-three of the 25 types were represented in the 1990 sample (Table 1).

In the original classification of the 1981 sample (Whitney and Miller 1987a), I required that each defined song type be shared by two or more birds in the sample. Thus, for each

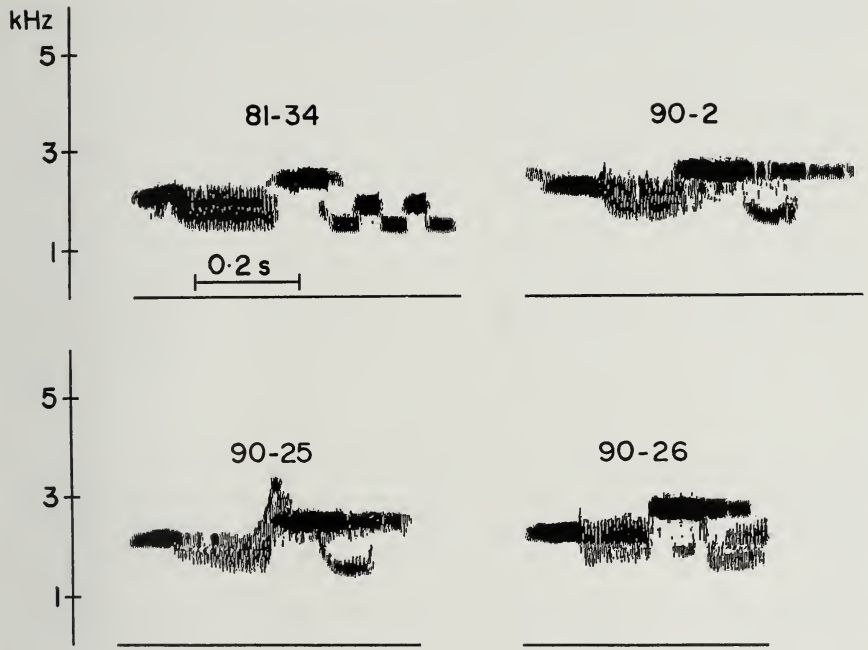

FIG. 1. Type 16 B phrase from 1981 (top left) and three unclassified phrases from 1990.

type there was evidence of learning by imitation. If the same criterion is applied to the 1990 sample, one additional song type must be defined. This type, resembling a variant of Type 16 that lacks a terminal trill, was shared by three birds (Fig. 1).

Superficially, the relative abundances of the different types appear similar for 1981 and 1990 (Table 1). Type 1 was the most common type in both samples, and Types 4, 6, 8, 12, 13, 16, and 23 were among the 10 most common types in both samples. The Spearman rank correlation between the two samples is 0.81 ($P < 0.001$). Despite this significant correlation, the possibility remains that the samples differ subtly. To check for such differences, I used a G-test (Zar 1984) to compare the samples with respect to the abundances of the eight most common (both samples combined) song types. These eight types included all those for which the expected abundances were greater than five. The results indicate no difference between the samples ($G = 7.14$, df = 7, $P > 0.25$).

Using multivariate analysis of variance (from the SYSTAT statistical package), I compared the structure of Type 1 B phrases in the two samples. A typical Type 1 phrase consists of a sequence of four unmodulated notes, each sustained on a relatively constant frequency (see fig. 4 of Whitney 1989). The analysis was based on the following seven parameters of Type 1 phrases: (1–3) time from the onset of each of the first three notes to the onset of the following note, and (4–7) dominant frequency of each note, taken 0.05 sec after the onset of the note.

For each of these parameters, the difference between the two years was only slight (Table 2), and the results of the analysis of variance showed no significant difference between the 1981 and 1990 phrases ($F = 0.67$, df = 7, 27, $P = 0.70$).

TABLE 1
ABUNDANCES OF SONG TYPES IN THE 1981 AND 1990 SAMPLES

Type	1981		1990	
	Abundance	Percent	Abundance	Percent
1	20	13.0	15	13.2
2	2	1.3	1	0.9
3	3	1.9	1	0.9
4	14	9.1	9	7.9
5	5	3.2	3	2.6
6	6	3.9	4	3.5
7	4	2.6	2	1.8
8	11	7.1	9	7.9
9	3	1.9	0	0.0
10	3	1.9	8	7.0
11	4	2.6	3	2.6
12	7	4.5	9	7.9
13	9	5.8	10	8.8
14	6	3.9	3	2.6
15	2	1.3	1	0.9
16	10	6.5	4	3.5
17	2	1.3	1	0.9
18	3	1.9	2	1.8
19	3	1.9	5	4.4
20	3	1.9	1	0.9
21	5	3.2	2	1.8
22	2	1.3	1	0.9
23	8	5.2	10	8.8
24	3	1.9	1	0.9
25	3	1.9	0	0.0
Unclassified	13	8.4	9	7.9
Total	154	100.0	114	100.0

Discussion.—The results demonstrate a striking similarity of song between the two samples: (1) of 25 song types defined for the 1981 sample, 23 were found in 1990, (2) the relative abundances of the different song types were the same in the two samples, and (3) according to a multivariate analysis of variance, the structure of the most common song type was the same in the two samples. The only discernable difference between the two samples was the presence in 1990 of one song type that was absent in 1981. These results are consistent with those of the earlier longitudinal study (Whitney and Miller 1987a). In that study, 12 of the 13 song types recorded in Sapsucker Woods in 1969 (N = 11 birds) were present in 1981 (N = 16 birds), together with four new types. The relative abundances of the different types were significantly correlated in the two samples. The results are also consistent with earlier reports of a lack of geographical variation in Wood Thrush song (Whitney and Miller 1987a, Whitney 1989).

Thus, compared with other songbirds that have been studied in detail (see references above), Wood Thrushes appear to have song that is unusually resistant to change. This

TABLE 2
PARAMETER VALUES[a]

Parameter	1981[b]	1990[c]
Onset of 1st note to onset of 2nd note (s)	0.12 ± 0.004	0.12 ± 0.006
Onset of 2nd note to onset of 3rd note (s)	0.13 ± 0.005	0.12 ± 0.007
Onset of 3rd note to onset of 4th note (s)	0.10 ± 0.007	0.11 ± 0.006
Dominant frequency of 1st note (Hz)	2540 ± 97.5	2500 ± 138.9
Dominant frequency of 2nd note (Hz)	2000 ± 89.3	2050 ± 127.3
Dominant frequency of 3rd note (Hz)	3450 ± 139.6	3400 ± 167.9
Dominant frequency of 4th note (Hz)	2900 ± 122.2	2900 ± 152.5

[a] All values are means ± SE.
[b] N = 20.
[c] N = 15.

resistance evidently does not result from a lack of "mutant" songs as raw material for evolution, since 8% of the songs in each sample were unclassified (Table 1; see also table 1 of Whitney and Miller 1987a). Perhaps, as I have proposed elsewhere (Whitney and Miller 1987a), mutant songs are at a selective disadvantage in the cultural transmission of Wood Thrush song.

This hypothesis can account for the lack of success of mutant songs but not for the apparent stability over a nine-year period in the relative abundances of the 25 defined song types. It seems plausible that a frequency dependent process is responsible for this stability. For example, the probability of a given song type being learned might be inversely related to the relative abundance of that type in the population (Whitney and Miller 1987a). Other frequency-dependent mechanisms are also possible. Reporting on a study of Darwin's Medium Ground Finches (*Geospiza fortis*), Gibbs (1990) proposed that males with rare song types might be more easily recognized by neighbors and thus at an advantage over males with common song types.

An alternative hypothesis invokes dispersal to account for the lack of geographical variation in Wood Thrush song (Whitney 1989). This hypothesis can be applied as follows to the present results: If male Wood Thrushes learn their songs while still in their natal areas, subsequent dispersal would have a retarding effect on temporal change in song. Suppose (in the simplest case) that all songs, including mutant ones, are selectively neutral. Within a local area, some mutant songs would be learned by fledgling males, but the continual turnover of mutant songs would act as a brake on directional evolution of song in the area. The first step in testing this hypothesis should be to evaluate the assumption that male Wood Thrushes learn their songs before dispersal from natal areas. Two points regarding this assumption can be made here: (1) within a local population the degree of song type sharing does not vary as a function of the distance between males, suggesting that little or no learning occurs after males have settled on breeding territories (Whitney and Miller 1987a). The possibility remains that learning occurs after dispersal but before males settle on territories. (2) Captive Wood Thrushes are able to learn B phrase repertoires of normal size and complexity when tutored with recorded song between the ages of 20 and 80 days (Whitney and Miller 1987b). These results are consistent with the assumption, but a critical test will require detailed field studies (see, e.g., Payne et al. 1981).

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CARL L. WHITNEY, *Dept. of Biology, College of Charleston, Charleston, South Carolina, 29424* (address to which reprint requests should be sent) *and Rockefeller Univ. Field Research Center, Millbrook, New York 12545.* *Received 22 Oct. 1991, accepted 16 Jan. 1992.*

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Egg destruction by Eastern Meadowlarks.—Destruction of eggs by passerines is a relatively rare phenomenon confined mainly to the Troglodytidae and Mimidae. Egg pecking has been reported for Marsh Wrens (*Cistothorus palustris*; Allen 1914; Verner 1975; Picman 1977a, b; Bump 1986), Sedge Wrens (*C. platensis*; Picman and Picman 1980), House Wrens (*Troglodytes aedon*; Kendeigh 1941, Belles-Isles and Picman 1986a), Bewick's Wrens (*Thryomanes bewickii*; J. Picman, unpubl. data), Cactus Wrens (*Campylorhynchus brunneicapillus*; Anderson and Anderson 1973), Gray Catbirds (*Dumetella carolinensis*; Belles-Isles and Picman 1986b), and four species of Galapagos mockingbirds (*Nesomimus* spp.; Bowman

and Carter 1971). In addition, at least two icterid species are also known to destroy eggs. Female Brown-headed Cowbirds (*Molothrus ater*) frequently remove one or more eggs from clutches of their hosts (e.g., Hann 1937, Mayfield 1977) and male cowbirds also seem to destroy eggs (Burgham and Picman, unpubl. data). Finally, Creighton and Porter (1974) and Schaeff and Picman (1988) observed Western Meadowlarks (*Sturnella neglecta*) destroying Horned Lark (*Eremophila alpestris*), Lark Bunting (*Calamospiza melanocorys*), and Japanese Quail (*Coturnix coturnix*) eggs.

The relative rarity of egg pecking among passerines could suggest high costs or low rewards associated with this behavior. For instance, egg-destroying activities may expose a given individual to aggression from the nest owners that may sometimes be much larger than the aggressor (Burt 1970, Picman 1983, Bump 1986). When egg pecking occurs despite such costs, the egg peckers probably derive some compensating advantage that may be sufficiently great in certain circumstances.

Theoretically, egg pecking should be favored when competition for limited resources is intense and the species involved cannot reduce competition through resource partitioning. This situation is likely to occur in simple, two-dimensional habitats where low food diversity and structural simplicity of the habitat preclude specialization. In such a situation, interspecific aggression promoting interspecific territoriality should be favored (Orians and Willson 1964). The egg-destroying behavior, as a mechanism of interference competition, should also be more frequently exhibited by species breeding in simple two-dimensional habitats such as marshes, savannahs, old fields, and meadows.

In 1986, I examined predation on artificial passerine nests in different habitats. Predation experiments conducted in a meadow habitat revealed that Eastern Meadowlarks (*Sturnella magna*) destroyed eggs placed in experimental nests. Because this is, to my knowledge, the first record of egg destruction by Eastern Meadowlarks, in this note I describe egg-pecking behavior of Eastern Meadowlarks from pictures of predation events, estimate the importance of meadowlarks as egg predators relative to other nest predators, and discuss the adaptive value of egg destruction by this species.

Methods.—Results were obtained during a study of predation patterns on passerine nests conducted from May to August 1986 in the Mer Bleue Bog conservation area near Ottawa, Ontario. To identify predators operating in the meadow, I used 10 automatic camera setups. These will take pictures of predators manipulating Japanese Quail eggs placed on a trigger in an experimental nest (see Picman 1987). The cameras (placed 25 cm above the ground) with experimental nests (placed on the ground) were distributed 10 m apart along a transect that was 20 m from any of the experimental quadrats described below. The camera transect was moved to a new location every 10 days, so that a fairly large area was sampled. The camera setups were visited every 24 h (usually between 14:00 h and 16:00 h), and if predation had occurred, a new egg was placed in an experimental nest and the camera was reset.

To determine predation rates in a meadow habitat, I distributed artificial nests made of grass (see Picman 1987), each containing one fresh quail egg, throughout three 80 m × 80 m quadrats (quadrats were separated by at least 20 m). The artificial nests, resembling Red-winged Blackbird (*Agelaius phoeniceus*) nests in size and appearance, were placed on the ground and camouflaged with surrounding vegetation to simulate natural nests. In the first set of experiments, designed to examine the effect of nest dispersion on predation, I distributed nests (without cameras) in uniform, random, and clumped spacing patterns (40 nests per quadrat). The choice of nest sites in selected areas was determined by the availability of vegetation (i.e., nests were placed in dense vegetation where they could be better concealed). Each of the three quadrats received all three nest distributions at different times (i.e., three time series of these experiments were conducted). Experimental nests were examined for predation on days 2, 4, 6, and 8 after start, and destroyed eggs were not replaced.

TABLE 1
EGG PREDATORS, IN DECREASING ORDER OF SIGNIFICANCE, AND TYPE OF DAMAGE TO EXPERIMENTAL EGGS

Predator	No. of cases (% of total)	Description of egg damage
Skunk	102 (71)	Empty shells ranging from small fragments to ¾ of an egg; squeezed, flattened shells; in or within 40 cm of the nest
Eastern Meadowlark	32 (22)	Punctured eggs (holes 4–10 mm) with contents; broken eggs with most, some, or no contents, depending on the extent of egg damage; eggs usually in nest, sometimes 20–30 cm away from nest
Raccoon	5 (3)	Entire eggs always removed
Woodchuck	3 (2)	Broken, empty shell within 30 cm of the nest
Northern Harrier	1 (1)	The entire egg missing
American Crow	1 (1)	The entire egg missing
Total	144 (100)	

The subsequent time series of these experiments were separated by at least five days. In the second set of experiments, designed to examine the effect of prey density on nest predation patterns, 40, 20, and nine nests were distributed uniformly in the same quadrats as in the first set of experiments. In these experiments, each quadrat again received all three nest densities. Subsequent time series were separated by at least two days. In this paper, I combined results of both sets of experiments to examine overall nest predation rates and the effect of time in a season on predation.

Results.—The camera study yielded a total of 144 cases of predation events. The most important predators were striped skunks (*Mephitis mephitis*) which appeared in 102 (71%) cases. Skunks usually broke the quail eggs; the type of egg damage inflicted by skunks is described in Table 1. Eastern Meadowlarks appeared on 32 (22%) photos in pecking position. In most of these cases, birds in the photos were touching the egg with their beaks, suggesting that they had just pecked an egg placed on a trigger mechanism, thereby setting off the camera. Fourteen (44%) eggs destroyed by meadowlarks had one or two punctures (in 11 of these, egg contents were undisturbed, and in the remaining three, the yolk had been removed, but most of the albumen was intact). In 12 (38%) cases, only small pieces of shell were found in or near the nest. Finally, in six (19%) cases of meadowlark predation, one-half or more of the egg shell was found in the nest (in only one of these cases was some albumen still present in the shell). However, it is possible that in some of these 18 cases, during which the eggs were more extensively damaged, the meadowlark visit was followed by a visit from another predator such as the skunk. This is supported by the fact that in three of these cases, I found squeezed, empty egg shells at the nest. This type of egg damage is characteristic of skunk predation (Table 1). Finally, the remaining cases of predation involved raccoons (*Procyon lotor,* five cases), woodchucks (*Marmota monax,* three cases), a Northern Harrier (*Circus cyaneus,* one case), and an American Crow (*Corvus brachyrhynchos,* one case). The damage to eggs by these predators is described in Table 1.

Between 19 May and 5 August 1986, a total of 567 artificial nests with single quail eggs were offered to predators during six series of experiments in three quadrats. The predation

TABLE 2
PREDATION ON EXPERIMENTAL NESTS

Day	Cumulative No. (%) of depredated eggs	No. eggs that survived
2	123 (22)	444
4	204 (36)	363
6	259 (46)	308
8	323 (57)	244

rate was greatest in the first two days of exposure (Table 2). A cumulative total of 323 (57%) eggs were destroyed in the course of eight days of exposure.

Based on cumulative data by day eight of all experiments, predation rates varied from 30% to 91% among six samples (Table 3). The proportion of depredated nests differed significantly among experiments, and predation was generally higher in the second half of the breeding season (Table 3).

To estimate the relative importance of meadowlark predation, I examined the appearance of depredated eggs. Punctured eggs are characteristic of meadowlarks (Table 1) and thus were used as an index of meadowlark predation. In the six experiments, between 0 and 38% of all depredated eggs had one or two punctures. The highest proportion of punctured eggs was found between 7 and 15 July, late in the breeding season (Table 3), when I observed two adult meadowlarks and three juveniles on two of the three quadrats. The recently fledged juveniles were following adults foraging on the quadrats or in adjacent meadows. In addition, there was another pair staying relatively close to the study quadrats. When all experiments are combined, 31 of the 323 depredated eggs (10%) were merely punctured (Table 3). Egg contents were intact in all but one of these 31 eggs. This index may underestimate meadowlark predation, since many pecked eggs may show more damage (see above; Table 1). In the camera study, of all eggs depredated by meadowlarks, approximately 44% were merely punctured while 56% had more extensive damage. If similar rates apply to the six experiments done between May and July, it is possible that another 40 eggs were destroyed by this species.

TABLE 3
PREDATION ON QUAIL EGGS DURING SIX CONSECUTIVE EXPERIMENTS CONDUCTED BETWEEN 19 MAY AND 5 AUGUST, 1986

Experiment number	Date of start	No. (%) of depredated eggs	Total No. of nests	No. (%) depredated eggs with punctures
1	19 May	36 (30)	120	1 (3)
2	4 June	84 (70)	120	0 (0)
3	17 June	38 (32)	120	0 (0)
4	7 July	48 (70)	69	18 (38)
5	17 July	54 (78)	69	7 (13)
6	28 July	63 (91)	69	5 (8)
Total	—	323 (57)	567	31 (10)

The total estimate for the impact of meadowlarks on experimental clutches (i.e., punctured plus more damaged eggs) is thus 22% of all depredated eggs. The relative importance of the other predators, however, cannot be estimated from data on appearance of depredated nests because depredation signs are not unique for individual predators (see Table 1).

Discussion.—To my knowledge, this is the first record of egg destruction by Eastern Meadowlarks, although the closely related Western Meadowlark may destroy eggs and kill nestlings (Creighton and Porter 1974, Schaeff and Picman 1988). The two meadowlark species may thus exhibit similar nest-destroying tendencies.

Eastern Meadowlarks were the second most important predator (after striped skunks) responsible for more than 20% of all predation in the study area. This suggests that Eastern Meadowlarks could significantly affect the reproductive success of co-occurring birds such as Bobolinks (*Dolichonyx oryzivorus*), Red-winged Blackbirds, and Savannah Sparrows (*Passerculus sandwichensis*), that were present on or near the study quadrats.

In this study, a maximum of four adults and several fledglings could have been responsible for the destruction of eggs that could be ascribed to meadowlarks. Unfortunately, because meadowlarks in the study area were not individually marked and these birds sometimes moved long distances suggesting very large feeding territories, the number, sex, and age of individuals involved in predation events could not be determined.

Two hypotheses have been proposed to explain the occurrence of egg pecking by small passerines (Orians and Willson 1964; Verner 1975; Picman 1977a, b; Picman and Picman 1980; Belles-Isles and Picman 1986 a, b). First, eggs are an important food source, and egg destruction is a form of predation. Second, through destruction of clutches of competitors, birds may achieve partial or complete interspecific territoriality, thereby reducing competition for limited resources. In general, the "competition hypothesis" offers a more plausible explanation for more intensively studied species such as Marsh Wrens for several reasons. First, individuals of the species exhibiting egg-destroying behavior rarely consume egg contents (Picman 1977a, b; Picman and Picman 1980; Belles-Isles and Picman 1986a, b). Second, species involved may exhibit complete or partial interspecific territoriality (e.g., Burt 1970, Verner 1975, Picman 1980, Bump 1986), presumably as a result of interspecific interactions (Leonard and Picman 1986). Third, some of these species also kill small nestlings without eating their flesh (e.g., Picman 1977a, b; Belles-Isles and Picman 1986a; Bump 1986). Fourth, egg-pecking responses may be influenced by the prevailing type of competition (i.e., intra- vs interspecific competition; Picman 1984).

The fact that contents of many eggs attacked by Eastern Meadowlarks seemed intact is more consistent with the competition hypothesis. However, the two hypotheses are not mutually exclusive and thus the final test will require more data on the frequency of egg pecking and egg consumption as a function of food availability, the frequency of egg destruction as a function of intensity of competition for limited resources, and the effect of egg destruction by meadowlarks on distribution of other co-occurring species.

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Jaroslav Picman, *Dept. of Biology, Univ. of Ottawa, 30 Marie Curie, Ottawa, Ontario K1N 6N5, Canada.* *Received 9 April 1991, accepted 6 Feb. 1992.*

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Influence of nest cover on habitat selection in Clay-colored Sparrows.—Prevailing hypotheses (Rosenzweig 1981, 1985; Conner et al. 1986) contend that feeding opportunity is the primary influence on habitat selection in birds. Feeding opportunity may indeed determine habitat selection for many bird species because birds, in general, must feed themselves

and their young on food available within their territories. Clay-colored Sparrows, however, forage only outside their breeding territories (Knapton 1979, 1980). They stake their unusually small (1000 m^2) territories in dense stands of low shrubs and fly to distant grasslands or cultivated fields to forage (Knapton 1979). Thus, the prevailing hypotheses on habitat selection apparently do not apply to Clay-colored Sparrows. Nonetheless, in the absence of foraging pressures, territorial Clay-colored Sparrows still prefer certain habitat features and avoid others (Walkinshaw 1939, Knapton 1979). In Manitoba, for example, Knapton (1979) observed that the low shrub *Symphoricarpos occidentalis* dominated vegetation within territories; he identified this shrub as a limiting resource because territory size and shrub density were negatively correlated.

Martin and Roper (1988) proposed an alternative hypothesis that the main determinant of habitat selection for some bird species is nest cover. Indeed, high quality nest cover can improve the territory-holder's fitness by reducing both nest predation (Yahner and Cypher 1986, Martin and Roper 1988) and mortality of nestlings due to harsh weather (Calder 1973, Walsberg 1981). If nest cover determines habitat selection in Clay-colored Sparrows, then the habitat features males include in their territories should have high value as nest cover relative to available habitat features. I tested this prediction by comparing vegetation within and outside the territories.

Study area and methods.—The study area was part of a 226-km^2 grassland in Buena Vista Township, Portage County, central Wisconsin (44°17′N, 89°34′W). Before being drained, this grassland was a tamarack (*Larix laricina*) swamp with acidic, organic soils (Hamerstrom and Hamerstrom 1973). The Wisconsin Dept. of Natural Resources now manages the grassland for threatened Greater Prairie Chickens (*Tympanuchus cupido*) by burning, tillage, and grazing (J. Kier, pers. comm.).

Vegetation data were collected in August 1990 when plants were mature enough to be identified. Following Zimmerman (1988), I chose six square 10-ha plots and sampled vegetation randomly within these plots. Each of the plots contained two linear transects, 324 m in length, separated by at least 18 m. I began these transects randomly 18 m internal to a plot's southern or western border and proceeded along a line perpendicular to that border. Each transect contained a random number (N = 2–18) of sample points. (No more than 18 sample points could fit on a transect plot's width.) In all, I established 12 transects and 103 sample points. At each sample point, I recorded percent cover for herbaceous plants, using a 0.10 m Daubenmire frame (Daubenmire 1968). For woody plants, I used a square quadrat (Cottam and Curtis 1956) measuring two m on a side. In the quadrat, I also measured vegetation height using the tallest plant, alive or dead. Vertical density was measured by counting plant contacts on a vertical 12 mm diameter rod. This measurement was made only when wind speed was less than 25 km/h, in order to minimize extraneous plant contacts. Relative importance (I) for each plant type was calculated with Daubenmire values as $I = F + (C/100)$, where F is the plant's frequency of occurrence, expressed as a decimal, and C is its percent coverage. Each vegetative feature was designated as either high value or low value nest cover, following Knapton (1978, 1979, 1980) who found that the sparrows prefer nesting below one m in dense shrubs. The nests I found during vegetation sampling confirmed this preference (Munson, unpubl. data).

I observed an estimated 60–70 unbanded male Clay-colored Sparrows for 16 h in May 1991 to determine territorial boundaries. For each sample point, I made at least two, five-min visits, during which I watched for indications that the point was within a territory. If a bird sang or chased a conspecific intruder, its location was marked on a large-scale map that included, as marks of reference, the 103 sample points. This spot-mapping benefitted from the conspicuous and energetic behavior of territorial males, and consequently there were numerous points of observation per bird. I assumed this technique did not alter the

TABLE 1

RELATIVE IMPORTANCES (I) OF THE FIVE MOST ABUNDANT PLANTS OCCURRING WITHIN CLAY-COLORED SPARROW TERRITORIES

Plant	Frequency of occurrence (F)	Percent cover (C)	Relative importance (I)[a]
Solidago spp.	0.71	35	1.06
Spiraea alba	0.59	20	0.79
Poa compressa	0.47	29	0.76
Linaria vulgaris	0.57	12	0.69
Phalaris arundinacea	0.27	20	0.47

[a] Relative importance was calculated as F + (C/100), where F is frequency of occurrence, expressed as a decimal fraction, and C is percent coverage.

sparrows' behavior, because the birds tolerate human activity (Knapton 1979; Munson, pers. obs.). The minimum convex polygon method (Mohr 1947) was used to infer territorial boundaries from points of observation. I compared habitat inside territories to that outside territories by conducting two-sample *t*-tests for the following measurements: woody stem density, vegetation height, percent coverage by each plant, vertical density, and species richness. To compare frequencies of occurrence for each plant, I used goodness-of-fit chi-square tests.

Results and discussion.—Of 103 sample points, 49 were within and 54 were outside of territories. Fifty-eight kinds of plants were recorded in sampling, 42 of which occurred within territories. The five plants of greatest importance within territories (Table 1) covered 116% of an average territory, a coverage in excess of 100% because leaves overlapped. Some plants of lesser importance, such as *Salix interior,* may still be crucial elements of territories judging from the sparrows' preference for them. Eleven habitat features were "preferred," which I define as more abundant inside than outside of territories. I divided these habitat features into high value and low value nest cover (Table 2). Eight of the 11 preferred habitat features had high value as nest cover. Conversely, none of the three habitat features that were more abundant outside of territories had high value as nest cover. Habitat features not displayed in Table 2 showed no statistical difference between the samples within and outside territories. These habitat features were: percent cover for 44 additional species of plants, stem density for seven species of woody plants, and frequency of occurrence for 53 species of plants.

Clay-colored Sparrows selected territories containing dense stands of woody vegetation and avoided open grasslands. Grasses formed an important vegetative component within territories, but three of the seven recorded grass species were more common outside territories. *Poa compressa* and *Agropyron repens* had greater coverages, and *Phleum pratense* occurred with greater frequency outside of territories (Table 2). I could not relate the importance of woody plants with that of grasses because abundance of grasses was measured in percent cover, whereas woody plants were measured with stem densities. Nevertheless, stem densities for *Salix interior* and *Spiraea alba* were much greater within territories, and their shade may have suppressed the importance of grasses within territories. Thus, the birds' apparent aversion to grasses may have been only an artifact of their selection for woody vegetation.

The results presented in Table 2 support the prediction that in Clay-colored Sparrows preferred habitat features are of high value as nest cover rather than a reflection of what is

TABLE 2
HABITAT WITHIN AND OUTSIDE OF CLAY-COLORED SPARROW TERRITORIES

Habitat feature	Within territories	Outside territories	P^b
Stem density (m^{-2})			
Salix interior[c,d]	1.8 ± 3.0[a]	0.02 ± 0.02	<0.0002
Spiraea alba[c,d]	7.6 ± 7.4	4.3 ± 8.4	<0.05
Percent cover (%)			
Agropyron repens	10.7 ± 21.4	30.9 ± 35.9	<0.001
Phalaris arundinacea[c]	20.1 ± 37.3	4.1 ± 17.7	<0.01
Poa compressa	29.3 ± 40.1	48.6 ± 42.2	<0.02
Frequency of occurrence			
Salix interior[c,d]	0.41	0.02	<0.0002
Phalaris arundinacea[c]	0.27	0.06	<0.02
Spiraea alba[c,d]	0.78	0.33	<0.02
Carex sp.[c]	0.08	0.00	<0.05
Phleum pratense	0.12	0.33	<0.05
Other			
Woody species richness[c,d]	1.9 ± 1.2	0.6 ± 0.6	<0.0001
Vegetation height (cm)[c,d]	186.3 ± 156.9	88.9 ± 17.3	<0.0002
Plant species richness[c,d]	5.7 ± 2.1	4.7 ± 1.7	<0.01
Vertical density (contacts)[c,d]	7.4 ± 2.3	6.4 ± 2.2	<0.05

[a] Mean ± SD.
[b] See Methods section for tests used.
[c] Value is greater within territories.
[d] Habitat feature of high value as nest cover.

available. Only 19% (22 of 118) of the habitat features available to the sparrows had high value as nest cover, and yet 73% (8 of 11) of the habitat features that were more abundant within territories were of high value as nest cover. The disparity is significant ($\chi^2 = 5.52$, $P < 0.02$) and provides evidence that the sparrows choose breeding habitat for its abundance of nest cover.

For the numerous bird species that both nest and forage within their territories, it is difficult to evaluate the relative influences that nest cover and feeding opportunities have on territorial habitat selection (Martin and Roper 1988). In Clay-colored Sparrows, however, individuals leave their territories to forage in a different habitat type (Knapton 1979). It is not known how far the foraging birds travel from their territories, but I have observed sparrows flying hundreds of meters to habitat patches completely disconnected from territories. Therefore, feeding opportunities apparently do not determine territorial habitat selection in this species. I have shown that in the absence of foraging demands, at least for Clay-colored Sparrows, nest cover may become the primary influence on territorial habitat selection. Still, both nest cover and feeding opportunities can conceivably influence avian habitat selection. In most bird species, the two influences likely operate concurrently, but among bird species the relative influences may vary considerably. Territorial habitat selection in Clay-colored Sparrows, evidently determined by nest cover and not food, would fall at an extreme on this continuum of influences.

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Erik S. Munson, *College of Natural Resources, Univ. of Wisconsin, Stevens Point, Wisconsin 54481.* (Present address: *Dept. of Ecology, Ethology, and Evolution, Univ. of Illinois, Champaign, Illinois 61820.*) *Received 8 Oct. 1991, accepted 15 Feb. 1992.*

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Dominance relationships of dabbling ducks wintering in Yucatan, Mexico.—Evolution of dominance behavior in waterfowl may be related to variation in the ability to obtain needed resources (e.g., food). This idea has been used to support hypotheses explaining differential distribution of the sexes (Nichols and Haramis 1980, Hepp and Hair 1984) and inter- and

intraspecific variation in pairing chronology (Paulus 1983). Knowledge of dominance in nonbreeding Anatinae is based on data obtained from temperate areas. Among Nearctic Anatinae, however, large numbers of Blue-winged Teal (*Anas discors*), Northern Pintails (*A. acuta*), Northern Shovelers (*A. clypeata*), and American Wigeon (*A. americana*) winter in the Neotropics (Bellrose 1980), where ecological conditions (most notably temperature) differ. Ducks wintering in the Neotropics may have reduced energetic demands because of mild temperatures (Thompson and Baldassarre 1990). Therefore, dominance patterns and/or pairing chronology might differ in the Neotropics as compared to more northerly wintering areas. We examined aggressive behavior of waterfowl wintering in Yucatan, Mexico, to determine if dominance patterns in the Neotropics are consistent with previous explanations of the effects of dominance on pairing chronology and differential distribution of the sexes.

Study area and methods.—We conducted our study in the Laguna de Celestun (Celestun Estuary) on the west coast of the Yucatan Peninsula near the village of Celestun, Yucatan (Thompson 1989). Celestun Estuary is part of the Yucatan Lagoons wetland complex, which is largely restricted to the north coast of the Yucatan Peninsula. The Yucatan Lagoons are a major wintering area for Nearctic Anatinae, where during 1970–1988 the total number of wintering waterfowl varied from a high of 320,325 in 1979 to a low of 43,930 in 1982 (Baldassarre et al. 1989). Data were collected from 7 October to 13 March, 1986–1987 and 1987–1988. Observations were made using focal individual and ad libitum sampling of randomly selected, unmarked Blue-winged Teal, Northern Shovelers, Northern Pintails, and American Wigeon (Altmann 1974). We used a 15–60× spotting scope to observe eight focal individuals of each species during each of four daily time blocks of equal length on two of every three days. Days were defined as 0.5 h before sunrise to 0.5 h after sunset. Individuals were observed for 5 min each from five widely separated blinds or from a parked vehicle. Individuals were selected by pointing a 15–60× spotting scope toward a flock and selecting the bird closest to the center of vision. Flocks were selected by partitioning the area around the observation site into four equal zones and randomly selecting, without replacement, one zone per time block. Species selection was randomized within blocks, and sampling days were assigned randomly, without replacement, to blinds. Ad libitum sampling was used to record observations of aggressive interactions not involving focal birds (Thompson 1989). Sex ratios were determined every 7–10 days by recording the species and sex of all individuals within 100 m of a given observation blind.

All intra- and interspecific aggressive interactions were recorded, for which four levels of intensity were categorized as (1) Supplant—one individual moved into an area and the other moved away without confrontation, (2) Threat—open bill threats and jabs with the bill, (3) Chasing—one bird rushed another, causing it to move rapidly away, and (4) Fighting—biting and striking with the wings (modified from Paulus 1983, Hepp and Hair 1984, Alexander 1987). For each interaction, we recorded species, sex, and pair status of both participants, winner and loser, initiator of interaction, activity associated with the encounter, and the activity of both participants immediately following the encounter. Pair status was determined using criteria outlined by Hepp and Hair (1983) which were sustained proximity to a member of the opposite sex, inciting by the female, following of a particular male by a female, and male defense of the female. We estimated the percentage of all females that were paired each month by determining the pair status of females chosen for focal individual sampling and calculating the percentage of individuals that were paired.

We used *G*-tests (Sokal and Rohlf 1969) to determine if observed frequencies of initiating or winning an encounter differed from expected values in relation to individuals of dissimilar pair status or sex. We considered a species/pair status/sex group to be dominant over another group if they won more interactions than expected by chance (Hepp and Hair 1984, Alexander 1987).

TABLE 1

AGGRESSIVE INTERACTIONS OBSERVED AMONG SPECIES OF DABBLING DUCKS WINTERING IN YUCATAN, MEXICO, 1986–1988[a]

Species attacking	Species attacked				
	BWT[b]	NS	NP	AW	Total
Blue-winged Teal	556	25	13	0	594
Northern Shoveler	49	248	46	4	347
Northern Pintail	18	19	418	3	458
American Wigeon	2	18	0	123	143
Total	625	310	477	130	1542

[a] Total time (h) of focal individual sampling: BWT 368, NS 383, NP 275, AW 147.
[b] BWT = Blue-winged Teal, NS = Northern Shoveler, NP = Northern Pintail, AW = American Wigeon.

Results.—Of 1542 agonistic encounters observed, 87.2% were intraspecific (Table 1) and 97.1% were between birds of similar pair status. However, few individuals of each species paired while in Yucatan. For example, of 4417 Blue-winged Teal and 4951 Northern Shovelers observed during focal sampling, none were paired during winter (Oct–Mar), and only 2.5% of 3300 female Northern Pintails had paired by February. Among American Wigeon, females were first observed paired in December (6.0%; N = 447), 11.0% were paired in January (N = 82), 22.0% in February (N = 480), and 32.0% in March (N = 311). For each species, there was no difference (ANOVA; $P > 0.05$) between years in patterns of aggressive behavior. Encounters involving two groups of paired birds were rare (N = 6). Most aggressive interactions for each species were associated with feeding activity (54.7–80.6%), which suggests that competition for food may have been a proximate cause for aggression. To test this, we compared the percentage of encounters associated with each activity to expected values based on the proportion of diurnal time spent in each activity. For all species, the proportion of encounters associated with each activity differed (G-test; $P < 0.001$) from expected values, and interactions associated with feeding were more frequent than expected (feeding = 40.9–45.1% of diurnal activity; Thompson and Baldassarre 1991). The remaining interactions involved birds that were locomoting (11.0–23.1%), preening (3.0–8.2%), resting (1.7–5.0%), and courting (0.4–3.9%), but no obvious patterns were apparent for activities other than feeding. Encounters were brief (1–2 sec), and the losing individual almost always moved only a few (1–3) m away, performed a comfort movement (wing flap or stretch), and then resumed its previous activity. Among all species, threats were the most common

TABLE 2

PERCENTAGE OF EACH TYPE OF AGONISTIC BEHAVIOR OBSERVED IN DABBLING DUCKS

Species	Supplant	Threat	Chase	Fight
Blue-winged Teal	16.9	62.0	7.7	13.4
Northern Shoveler	11.3	71.3	14.6	2.8
Northern Pintail	18.4	56.6	9.8	15.2
American Wigeon	7.8	74.5	16.7	1.0

Table 3

Observed Sex Ratios of Waterfowl Wintering in Yucatan, Mexico, 1986–1988

	Species			
	BWT[a] (19)[b]	NS (19)	NP (20)	AW (10)
Total birds observed	1172	2830	2072	364
Percent males	75.7	64.6	84.4	66.8
Ratio males : female	3.1:1	1.8:1	5.4:1	2.0:1

[a] See Fig. 1.
[b] Number of samples.

agonistic display (56.6–74.5%), whereas the frequency of other displays varied among species (Table 2). Supplanting was probably under-recorded because it often was a subtle interaction.

Among all species, when pair status of participants was similar, the initiator won more interactions than expected by chance (Blue-winged Teal 91.2%, Northern Shoveler 94.7%, Northern Pintail 91.2%, American Wigeon 99.0%; $P < 0.001$). Females were more likely to initiate an intersexual encounter (56.1–61.5%; $P < 0.01$; Tables 3, 4) and, except for American Wigeon, won more interactions than expected (females won 57.2% Blue-winged Teal, 53.7% Northern Shoveler, 56.3% Northern Pintail; $P < 0.05$). Male and female American Wigeon won similar ($P > 0.05$) numbers of interactions (i.e., females won 46.0%), but sample size was small (N = 26). All encounters between birds of dissimilar pair status (N = 44) were intraspecific, and all were initiated by paired individuals. Paired males won 23 of 24 ($P < 0.001$) encounters with unpaired birds (19 of 20 with males, 4 of 4 with females), and paired females won 19 of 20 ($P < 0.001$) encounters with unpaired birds (13 of 14 with males, 6 of 6 with females).

Except for American Wigeon, participation by sexes in aggressive interactions differed ($P < 0.01$) from expected values. Female Blue-winged Teal, Northern Shovelers, and Northern Pintails participated in a greater proportion of interactions than expected, based on their proportion in the population. Male-male interactions in these species were less frequent,

Table 4

Frequency of Aggressive Interactions Observed by Sex and Expected Values Based on Population Sex Ratios

	Species							
	BWT[b]		NS		NP		AW	
Interaction	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Male-male	173	212	95	102	262	290	42	45
Female-female	54	22	52	31	43	10	16	11
Male-female	55	68	43	56	43	54	17	23
Female-male	88	68	55	56	60	54	27	23
G-scores	48.7***		15.6**		65.3***		4.6	

[a] Expected frequency = (proportion of first sex in population) × (proportion of second sex in population) × (total observations) (Hepp and Hair 1984).
[b] See Fig. 1.
** $P < 0.005$; *** $P < 0.001$.

TABLE 5

OVERALL PARTICIPATION IN AGGRESSIVE INTERACTIONS OBSERVED AND EXPECTED VALUES CALCULATED USING POPULATION SEX RATIOS OF MALE AND FEMALE WATERFOWL

	Species							
	BWT[b]		NS		NP		AW	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Male	489	560	288	317	627	689	128	136
Female	251	180	202	173	189	127	76	68
G-scores	34.3***		7.34*		32.01***		1.38	

[a] Expected frequencies = (proportion of sex in population) × (total observations) (Hepp and Hair 1984).
[b] See Fig. 1.
*** $P < 0.001$, * $P < 0.01$.

and female-female interactions more frequent than expected. Similarly, except in Northern Shovelers, female-male (female initiated) interactions occurred more often, and male-female interactions occurred less often than expected. Deviations from expected values were relatively greater in Blue-winged Teal and Northern Pintails, species exhibiting more biased sex ratios. This is supported further by comparing the overall participation in agonistic activities for each sex (Table 5).

Discussion.—Our data are similar to those of other studies of dominance behavior in nonbreeding Anatinae in that paired birds dominated unpaired birds, although few individuals paired during winter in Yucatan. Of more significance, however, was the lack of male dominance in Yucatan. For example, Hepp and Hair (1984) reported that in six species of dabbling ducks wintering in North Carolina, including three common to our study (American Wigeon, Northern Pintail, Northern Shoveler), males won more intersexual aggressive interactions than expected by chance and thus were dominant to females. In contrast, we found that females won more encounters than males (except American Wigeon) and were more likely to initiate an encounter than expected based on their proportion in the population. Ducks that initiate aggressive encounters usually win, which suggests that individuals assess the dominance status of other flock members, and only initiate encounters when they are likely to be successful (Patterson 1977). Consequently, we conclude that, except for American Wigeon, dabbling duck females are dominant to males in Yucatan.

Explanations for these patterns are unclear, because the costs and benefits of dominance rank are certainly complex (Hepp 1989). However, that male ducks wintering in Yucatan might be of lower dominance rank than males wintering at more northern latitudes could be expected if behavioral dominance plays a role in the differential distribution of wintering birds. For instance, Gauthreaux (1978:30) suggested that if the non-breeding range of a species is geographically disjunct from the breeding range, dominants should acquire those areas of highest quality closest to the breeding grounds. Subordinates, therefore, might be forced into areas farther from the breeding grounds or into habitats of lesser quality, especially when food is limited (Hepp 1989). Thus, if dominant ducks (i.e., high ranking males; Hepp and Hair 1984, Alexander 1987, Perry et al. 1988) are distributed farther north in winter than subordinates (i.e., unpaired females and low ranking males), females in Yucatan may be subordinate to males wintering at northern latitudes but of higher or equal (i.e., American Wigeon) rank than sympatric low ranking males, and thus dominant to them. Therefore, we believe the dominance patterns we observed are consistent with the hypothesis

that dominance can influence the differential distribution of the sexes because females, by wintering in Yucatan, could successfully compete for needed resources.

In many species of ducks, males predominate in northern areas during winter (see Hepp and Hair 1984), but the sex ratios in Yucatan do not support the prediction that females, because they are generally subordinate to males, predominate in southerly wintering areas. Indeed, sex ratios of dabbling ducks in Yucatan were similar to, if not more male-biased than, those reported from more northern areas (Bellrose et al. 1961, Hepp and Hair 1984, Miller 1985). This is interesting because, with the exception of Blue-winged Teal, Yucatan is near the southern extent of the wintering range for species in this study. Blue-winged Teal winter well south of Yucatan, and patterns may differ for teal wintering farther south. However, as noted by Hepp and Hair (1984:256), the hypothesis that dominance influences distribution does not predict the direction of dispersal. Rather, several factors (e.g., habitat suitability) probably interact to influence the distribution of sexes (Ketterson and Nolan 1983, Hepp 1989). Hepp (1989) demonstrated that age influenced the effect of sex on dominance rank of American Black Ducks; adult females were dominant to juvenile males but not to adult males. This may imply that juvenile males were more prevalent in winter populations of ducks in Yucatan than they are at more northern latitudes. We collected data from a limited number of ducks killed by hunters each year to test this idea. Combining years, the age ratio (adults to juveniles) for Blue-winged Teal was 74:36 for males and 39:43 for females and for Northern Pintails it was 7:11 for males and 7:14 for females. However, without data on American Wigeon and Northern Shovelers and more information on Pintails, the age ratio information is inconclusive.

In contrast to Yucatan, Hepp and Hair (1983:678) noted that >84% of American Wigeon wintering in North Carolina were paired in January, and >96% of Northern Pintails and Northern Shovelers were paired in February. Chronology of pair formation in Blue-winged Teal is not well documented, but observations indicate that pairing begins in late December or early January and continues until March (see Bluhm 1988, and others cited therein). Glover (1956) reported that 60% of Blue-winged Teal were paired upon arriving in northwest Iowa during late March.

Rohwer and Anderson (1988) reviewed potential costs and benefits of early pair formation and emphasized that pairing ultimately may benefit the female through protection by the male and increased dominance rank. Dominant birds also may be more successful at obtaining nutrients (if they are limiting) than subordinates, and thus may be in better condition and better able to survive stress associated with food shortage (Patterson 1977, Caraco 1979, Paulus 1983). In Yucatan, the few individuals that did pair were dominant to unpaired birds, which suggests that paired females should gain advantages similar to those potentially accrued by paired birds in other areas (i.e., farther north). However, females in Yucatan may not be willing to pair, if they are already dominant or equal in social status to males and thus probably have at least equal access to resources and do not need male protection. We believe that female dominance and lack of pairbonding in Yucatan relates to proposed female benefits and male costs of pairing in waterfowl but that patterns in the Neotropics are different from those in more temperate areas.

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JOHN D. THOMPSON AND GUY A. BALDASSARRE, *Environmental and Forest Biology, State Univ. of New York, College of Environmental Science and Forestry, Syracuse, New York 13210.* (Present address JDT: *Max McGraw Wildlife Foundation, P.O. Box 9, Dundee, Illinois 60118.*) *Received 21 Aug. 1991, accepted 1 Feb. 1992.*

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Dynamics of a year-round communal roost of Bald Eagles.—Communal roosts of Bald Eagles (*Haliaeetus leucocephalus*) occur regularly outside of breeding season and have been described in detail (Fitzner and Hanson 1979, Keister and Anthony 1983, Crenshaw and McClelland 1989). However, year-round Bald Eagle roosts have been studied only recently (Chester et al. 1990, Buehler et al. 1991). I describe here the results of 188 h of observation at a year-round communal roost of Bald Eagles in southern Florida.

Everglades National Park (ENP), located at the southern tip of the Florida peninsula, is home to a large, stable breeding population of Bald Eagles (ca 50 breeding pairs/year, Curnutt and W. B. Robertson, Jr., unpubl. data). The climate is sub-tropical with mean temperatures of 26.8°C in August and 18.9°C in January. Eagles nest in two major areas: Florida Bay, a shallow 1600 km^2 estuary, and the extensive mangrove forests of the park's Gulf coast. Nesting activity (nest building) begins in late November and ends (young fledged) in late March (Curnutt 1991). Bald Eagles have been known to use the southern end of the Miami Rock Ridge pinelands as a roosting site since they were discovered there in the early 1960s by A. Sprunt, IV, and W. B. Robertson, Jr. The southern terminus of the pinelands is nearly 20 km north of Florida Bay, the nearest Bald Eagle nesting and foraging habitat, and is dominated by mature slash pine (*Pinus eliottii*) with an understory kept open by natural and planned fires. During aerial surveys of the pinelands, I determined that roosting activity was concentrated in an area of ca 20 ha where the southern tip of the pine forest intersected the Main Park Road (MPR). The vegetation between the roost area and Florida Bay is dominated by dry *Muhlenbergia* prairie, red mangrove (*Rhizophora mangle*), and coastal prairie (Craighead 1971).

I observed the roost from atop a van on the MPR. I alternately parked and drove within 0.5 km of the road-pines intersection in order to count eagles. This allowed me to observe and count eagles perched at the edges and within the stands of pines. I observed the roost three consecutive evenings and the following mornings near the middle of each month from March 1990 through February 1991. The March 1990 observations were used to test and refine methods and are not included in analyses. I conducted evening observations from at least 1 h before sunset to 0.5 h after sunset and morning observations from 0.5 h before sunrise to 4 h after sunrise or until the last known eagle departed the area, whichever was later. I noted the direction of flight (bearing) and estimated altitude of each eagle seen flying. Times (to the nearest minute) were recorded for eagles entering or leaving the roost area. Trees in which I saw eagles perched were identified to species, noted as living or dead, and assigned to one of the following categories of relative height: above canopy, canopy height,

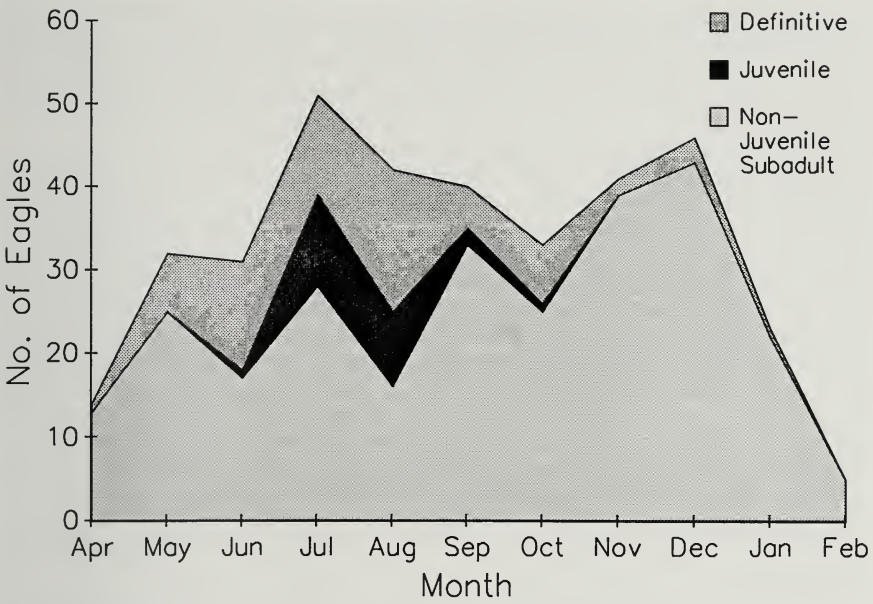

FIG. 1. Cumulative numbers of Bald Eagles observed each month at the Everglades National Park roost.

below canopy. When conditions of light and time allowed, I assigned each eagle to one of the six age classes described in McCollough (1989). This helped in identifying individuals during each observation period and avoiding double-counting. For analyses, eagles were considered either adult (definitive plumage) or subadult (all other plumages). Every 15 min I noted the temperature, wind speed and direction, percent cloud cover (to nearest 10%), and presence of precipitation. Days were considered cloudy if the average cloud cover was $\geq$75% and clear if the average was $\leq$25%. Effects of environmental conditions on eagles were analyzed using multiple linear regression. I used AbStat (copyright, Anderson-Bell Co. 1984) statistical package to analyze data. A probability level of 0.05 was considered significant.

I recorded 398 Bald Eagle sightings at the roost area during the study. I was able to assign 72% of the individuals to the age classes described by McCollough (1989). Aging in morning (AM) counts was more successful (78.8%) than in evening (PM) counts (63.6%) ($t = 2.53$, $df = 57$, $P = 0.01$) because of the better light conditions and longer observation time available in AM. The number of Bald Eagles observed in each observation period ranged from 0 to 18. There was no attempt to avoid double counting of individuals between observation periods. Comparisons between months are based on the cumulative number of eagles sighted during all PM and AM counts each month. Most (77%) of the eagle sightings were of subadults. There were two peaks in cumulative monthly eagle sightings at the roost (Fig. 1). The highest count, 54 in July, was brought about by the presence of adults and young of the year augmenting the subadult population. The second peak (47) occurred at the height of the breeding season in December and was composed primarily of subadults. The number of eagle sightings was lowest in February (5 subadults). The number of eagles arriving at the roost in the evening was negatively correlated with wind speed ($r = -0.68$, $df = 30$, P

= 0.004) and positively correlated with mean observation-period temperature ($r = 0.44$, df = 30, $P = 0.006$). There was no difference between the number of eagles arriving at the roost on evenings with south vs north winds (ANOVA, $F = 0.519$, df = 9, $P = 0.499$). The number of eagles observed during AM counts was directly related to the number observed arriving the night before ($r = 0.77$, df = 31, $P = 0.001$), suggesting that there was not a significant number of arrivals after 0.5 h past sunset.

The time that Bald Eagles arrived at the roost was strongly correlated with sunset ($r = 0.88$, df = 167, $P = 0.001$) and was not affected by cloud cover (clear vs cloudy evenings; ANOVA, $F = 0.63$, df = 86, $P = 0.533$). Arrival time was not significantly different for adults and subadults (ANOVA, $F = 1.83$, df = 159, $P = 0.178$). Adults tended to leave the roost later than subadults but the difference was not significant (subadult mean = 169.8 min after sunrise, adult mean = 191.2 min after sunrise, ANOVA, $F = 3.42$, df = 155, $P = 0.066$). Morning departure time was positively correlated with higher temperature ($r = 0.54$, df = 17, $P = 0.001$). Crenshaw and McClelland (1989) reported that eagles arrived later on clear evenings than on cloudy evenings at a roost in Montana, as did Lish (in Crenshaw and McClelland 1989) in Oklahoma. Crenshaw and McClelland (1989) also reported subadults leaving the roost earlier than adults and attributed this to poorer hunting skills of subadults and consequent lower food availability. Neither of these phenomena occurred at a significant level at the ENP roost. This may be attributed to the longer winter daylength in southern Florida resulting in greater foraging time. Unlike eagles in Montana (Crenshaw and McClelland 1989), ENP eagles rarely left the roost before sunrise and most returned before sunset.

Nearly all (95.8%) eagles arrived at the roost area from the south or southwest, regardless of the concurrent wind direction. Bearings of eagles leaving the roost in the morning showed more variability. Most (54.5%) flew south, with southwest and west accounting for another 20.1%. Departure bearings appeared to be influenced by wind direction as eagles soaring in thermals often drifted with the wind. The predominance of arrivals from and departures to the south and southwest indicate that most roosting eagles frequented northwestern Florida Bay. This area has the highest concentration of active Bald Eagle nesting territories in Florida Bay (Curnutt 1991) and is where a majority of subadults has been observed during annual aerial surveys of eagle nesting activity (W. B. Robertson, Jr., unpubl. data). Although Bald Eagle nesting in ENP occurs along the park's Gulf coast and among the brackish interior bays of the extreme southwestern peninsula, as well as in Florida Bay, eagles that visited the roost apparently frequented only Florida Bay.

Of the 393 Bald Eagle sightings, 216 involved birds perched in trees, all but one in slash pines. Both adults and subadults used super-canopy and canopy-level trees independently ($\chi^2 = 0.20$, df = 1, $P = 0.654$). There were two instances (<1%) of eagles perching in sub-canopy trees. Dead trees were used as perches 30.2% of the time.

Seasonal changes in the proportion of adult and subadult Bald Eagles as observed at the communal roost in ENP have not been reported for other areas. In Florida Bay, over 95% of 31 historical breeding territories have been occupied each breeding season (N = 31 seasons), although many of these (from 2–12/season) consisted of single (unpaired) adults (Curnutt 1991). Because Bald Eagles are highly territorial against conspecifics during the breeding season (Palmer 1988), adults would tend to stay at their territories during this time and perhaps drive subadults from the area. This would account for both the low incidence of adults and the higher numbers of subadults at the roost during the breeding season. Conversely, during the nonbreeding season subadults are free to spend more time at the undefended territories of Florida Bay, and adults (perhaps unpaired) are able to leave there and visit the roost. The low number of adults at the roost, even in the summer (maximum single observation period count = 6, July 1990) is a small proportion of the Florida Bay

adult population (ca 53). However, this would account for most of the unpaired adults (8) that defended territories during the 1989/1990 breeding season in Florida Bay (Curnutt 1991). Some of the variation in the numbers of eagles at the roost each month may be due to the presence of alternative roost sites (as in Buehler et al. 1991) of which I was unaware.

None of the Bald Eagles observed in this study was marked. The consistent movement to and from Florida Bay suggests that most of the eagles were part of the resident ENP population. However, since at least some Bald Eagles from every breeding population migrate (see Palmer 1988 for a review), it is possible that some of the eagles observed at the roost were migrants from other populations. Broley (1947) reported that young Bald Eagles, especially juveniles, dispersed from their natal area of the central Gulf coast of Florida during the summer in a generally northward migration. This was also found to occur with nestlings banded in central Florida (P. Wood, pers. comm.). Although the lower numbers of non-juvenile subadults at the roost in the summer may, in part, be due to migratory movements away from the area, the occurrence of subadult Bald Eagles, including juveniles, at the ENP roost from June to November suggests that some eagles fledged in Florida Bay may remain during the summer.

Unlike most Bald Eagle communal roosts, the ENP roost is not located near feeding areas, nor, with southern Florida's sub-tropical climate, does it seem to offer any obvious advantage in climate. The reason eagles visit the roost may be primarily social. Palmer (1988) suggested that pair formation among Bald Eagles can occur before definitive feathering and may come about through the extended association of pre-breeding individuals. At least one potential breeding pair (an adult male and Basic IV female) was formed at the ENP roost during this study. The high degree of interaction I observed between subadults, e.g., pursuit flights and talon grasping, as well as the increased level of aggression by eagles during the nesting season may facilitate mate selection. Bald Eagle prey in Florida Bay has included over 20 species of birds and over 10 species of fish (Curnutt, unpubl. data) and there is no indication that prey availability is a limiting or even stress-inducing factor for breeding eagles there (Curnutt 1991). The stable climate and food supply of Florida Bay has resulted in a saturated breeding population of Bald Eagles (Curnutt 1991) and, in turn, year-round social interaction at a communal roost.

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John L. Curnutt, *South Florida Research Center, Everglades National Park, Box 279, Homestead, Florida 33030.* *Received 16 Sept. 1991, accepted 7 Jan. 1992.*

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Nonbreeding Bald Eagle perch habitat on the northern Chesapeake Bay.—Bald Eagle (*Haliaeetus leucocephalus*) habitat is declining throughout much of the range because of human land uses along shoreline areas (Buehler et al. 1991a), logging (Anthony and Isaacs 1989), and recreation (Chester et al. 1990). Identification of habitat for protection requires knowledge of the characteristics that define habitat suitability. Although nesting and nocturnal roost habitat have been described throughout the eagles' range (e.g., Andrew and Mosher 1982, Keister and Anthony 1983, Anthony and Isaacs 1989, Bohall Wood et al. 1989, Buehler et al. 1991b), few studies have quantified diurnal perch habitat (Stalmaster and Newman 1979, Steenhof et al. 1980, Chester et al. 1990, Caton et al. 1992). Moreover, past studies relied on visual location of perched eagles along shoreline areas, potentially biasing results toward exposed, shoreline perch sites. We used radio telemetry to avoid this potential problem.

Except for Chester et al. (1990), other studies have not examined the effects of time of day or season on eagle habitat selection. Because microclimate variables such as temperature vary by time of day and season, we investigated whether diurnal perch selection differed with respect to these periods. We also tested the hypothesis that perch habitat differed from habitat available at random on the northern Chesapeake Bay.

Study area and methods.—The study area extended along the Chesapeake Bay from the Bay Bridge at Annapolis, Maryland, to the Conowingo Dam on the Susquehanna River, encompassing 3426 km^2. The area included 2472 km of bay, river, and creek shoreline and extended inland to the head of all major tributaries except the Susquehanna and Chester rivers. It also included part of the Baltimore metropolitan area and the U.S. Army Aberdeen Proving Ground, a 350-km^2 military installation. The study area included a largely urban-suburban setting near Baltimore, coastal lowland oak-gum (*Quercus* spp.-*Liquidambar styraciflua*) forests on the Aberdeen Proving Ground, agricultural fields with scattered oak woodlots on the Eastern Shore, and upland and lowland oak-gum-hickory (*Carya* spp.) forests along the Susquehanna River valley (Brown and Brown 1972).

A total of 59 Bald Eagles were radio-tagged. Twenty-nine immatures and two adults were trapped with floating noose-fish (Cain and Hodges 1989) and padded leghold traps (Young 1983) at Aberdeen Proving Ground, Susquehanna River, and Eastern Shore trap sites. Also, we radio-tagged 28 nestlings at 8–10 weeks of age in nests throughout the northern Chesapeake region.

Eagles were equipped with 65-g radio transmitters that had solar-charged nickel-cadmium batteries (Telemetry Systems, Inc., Mequon, Wis.) and an expected life of 4–5 years. We mounted radios dorsally on eagles with a 1-cm-wide teflon ribbon harness (Bally Ribbon Mills, Bally, Pa.).

Twice weekly during daylight, from March 1986 through June 1987, we located all radio-tagged eagles on the study area from fixed-wing aircraft, once during the early morning (sunrise to 09:15) and once during the remainder of the day up to 2 h before sunset.

For each perched eagle located, we photographed the perch tree with a single-lens reflex camera and used these photographs to relocate the perch trees on the ground. We visited each tree on foot and recorded tree species, diameter at breast height (dbh), and tree height (measured by clinometer). We estimated tree accessibility to a flying eagle as the total arc (0–360°) that was unobstructed by other tree canopies for a distance of 10 m from the trunk and 3 m below the perch tree's crown. We classed perch trees as live, dead, or dead-topped. We measured the height of the surrounding canopy with a clinometer. We sampled tree density at each site by counting all trees ≥10-cm dbh in an 11.3-m radius plot (0.04 ha) centered on the perch tree.

We measured the distance from the tree to the nearest habitat edge, defined as the intersection of forest, aquatic, human-developed, wetland, or agricultural habitats. We used the U.S. Geological Survey (USGS) land use and land cover database (Anderson et al. 1976) to classify cover type at each site as developed, forested, wetland, or agricultural. We calculated the area (ha) of each habitat block containing perches using ARC/INFO computer software. We also calculated the distance from each perch to the shoreline on a computer-digitized version of the USGS 7.5 minute topographic maps.

We divided the study-area shoreline into 2472 1-km sections and, using a random-numbers table, selected 178 sections. For each section selected, we randomly selected a distance between 0 and 1000 m along the section shoreline to define a point for comparison with eagle-selected sites. We chose the tree ≥20-cm dbh that was closest to each randomly selected shoreline point and measured the same characteristics that we measured for each perch tree.

We assigned perch trees to early morning leaf-on (sunrise–09:15, May–October), midday leaf-on (09:16–2 h before sunset, May–October), early morning leaf-off (sunrise–09:15, November–April) and midday leaf-off (09:16–2 h before sunset, November–April) classes, based on the date and time the tree was observed in use. We used Kruskal-Wallis tests to compare continuous variables among all classes of perch and randomly chosen trees, because variables were non-normally distributed. If the Kruskal-Wallis test resulted in the rejection of the null hypothesis ($P < 0.05$), we used Wilcoxon rank-sum tests to make pair-wise comparisons. We found no significant differences among perch tree classes in pair-wise comparisons ($0.06 < P < 0.98$) for all variables measured except for tree density. We pooled data, therefore, from all perch tree classes and compared all perch trees with randomly chosen trees. We used χ^2 analyses to compare the frequencies of discrete variables among perch trees and randomly chosen trees. We determined relative habitat preference based on Neu et al.'s (1974) approach.

Results.—We identified 220 Bald Eagle perch trees on the northern Chesapeake Bay (Table 1). Perch trees, on average, were larger in diameter, taller, extended farther above the canopy, and had greater accessibility than did randomly chosen trees ($P < 0.001$). Perch trees occurred in stands with greater canopy heights, were slightly farther from the edge, and occurred in stands with fewer trees per ha than did stands with randomly chosen trees ($P \leq 0.05$). Perch sites and randomly chosen sites were both relatively close to water ($P = 0.07$).

Eagles selected perches more often than expected in forested cover types, when compared to available sites, and eagles avoided human-developed types when compared to available

TABLE 1

CHARACTERISTICS OF BALD EAGLE PERCH TREES (N = 220) AND RANDOMLY CHOSEN SHORELINE TREES (N = 178), NORTHERN CHESAPEAKE BAY, MARYLAND

Variable	Perch trees			Randomly chosen trees			*P* value
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	
Diameter (cm)	56.8	1.5	19.5–132.5	34.5	1.0	20.0–84.5	<0.001
Height (m)	19.1	0.4	6.1–38.1	12.4	0.3	4.6–31.7	<0.001
Canopy height (m)	16.1	0.5	0–30.8	12.8	0.4	0–25.6	<0.001
Height above canopy (m)	3.0	0.4	−14.3–27.7	−0.4	0.4	−18.3–21.3	<0.001
Access (degrees)	262	6.0	0–360	223	7	0–360	<0.001
Trees per ha	554	34	25–5000	659	38	50–3750	<0.01
Distance to edge (m)	5	1	0–250	3	1	0–100	0.05
Distance to water (m)	46	7	0–704	34	4	0–553	0.07

TABLE 2

COVER TYPE, SPECIES COMPOSITION, AND CONDITION OF BALD EAGLE PERCH TREES (N = 220) AND RANDOMLY CHOSEN TREES (N = 178), NORTHERN CHESAPEAKE BAY, MARYLAND

Variable	Perch trees		Randomly chosen trees		Selection
	$\hat{p}$[a]	95% CI	$\hat{p}$[a]	95% CI	
Cover type					
Developed	4.1	0.8–7.4	19.7	12.2–27.2	−
Farmland	28.7	21.1–36.3	41.6	32.4–50.8	0
Forest	49.1	40.7–57.5	24.7	16.6–32.8	+
Wetland	18.2	11.7–24.7	14.0	7.5–20.5	0
Tree species					
Black locust	13.2	7.5–18.9	10.7	4.9–16.5	0
Oak spp.	22.3	15.3–29.3	22.5	14.7–30.3	0
Sweet gum	23.6	16.4–30.8	7.9	2.8–13.0	+
Yellow poplar	8.6	3.9–13.3	1.7	0.0–4.1	0
Other	32.3	24.4–40.2	57.3	48.0–66.6	−
Condition					
Live	50.0	41.6–58.4	92.7	87.8–97.6	−
Dead-topped	25.0	17.7–32.3	2.8	0.0–5.9	+
Dead	25.0	17.7–32.3	4.5	0.6–8.4	+

[a] $\hat{p}$ = proportion of trees in a given class of cover type, tree species, or condition.

sites (Table 2). Perch trees occurred in forest blocks larger in size than forests available along the shoreline ($\bar{x}$ = 1685 and 873 ha, respectively, $P = 0.02$). Eagles selected perches in sweet gums more than expected, based on availability, whereas eagles selected "other" tree species less than expected when compared to randomly chosen trees (Table 2). Oaks, black locusts (*Robinia pseudoacacia*), and yellow poplars (*Liriodendron tulipifera*) also were frequently used as perches, but not at rates greater than that expected, based on availability. Most perch trees were live, but eagles used a greater percent of dead or dead-topped trees than expected, based on availability (Table 2).

Discussion.—Eagles selected larger and more accessible trees for perching than what was available at random, similar to eagle behavior recorded elsewhere (e.g., McEwan and Hirth 1979, Stalmaster and Newman 1979, Steenhof et al. 1980, Keister and Anthony 1983, Anthony and Isaacs 1989, Chester et al. 1990). Unlike Chester et al.'s (1990) results for North Carolina, however, we found no structural differences between perches used in May–October and perches used during November–April. We also found no time of day effects. Because suitable conifers are nearly absent from the northern Chesapeake, eagles may not show the selection patterns Chester et al. (1990) found in mixed pine-hardwood forests in North Carolina (i.e., eagles selected pine perches after 11:00 during the leaf-on period). Other differences (e.g., eagles in North Carolina perched lower in the tree after 11:00) may be related to microclimate differences between the two areas. Eagles in North Carolina may seek shade during the heat of the day, whereas temperatures on the Chesapeake may not be hot enough to produce this behavior, except during the warmest days in summer. In addition, our analysis may have missed some of these effects by averaging conditions over

the entire leaf-off and leaf-on periods. Using similar seasonal definitions, however, we documented seasonal differences in roost habitat selection related to microclimate on the northern Chesapeake (Buehler et al. 1991b, c).

Most previous eagle habitat studies relied on visually locating eagles to identify used habitat and thus potentially biased results toward trees with more exposed perches. Because our results were similar to those from other studies, if a technique bias exists, it may not be significant, at least for the variables we measured. The key shortcoming of using surveys in which only shorelines can be observed is the inability to discover used inland habitats. On the northern Chesapeake, 11% of all diurnal radio-tagged eagle use occurred inland >80 m (range = 91–704 m). This disadvantage may be partly offset in areas with steep terrain where hillsides or mountainsides are still visible from the shoreline (Caton et al. 1992).

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David A. Buehler, Sheri K. Chandler, Timothy J. Mersmann, and James D. Fraser, *Dept. Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State Univ., Blacksburg, Virginia 24061*; and Janis K. D. Seegar, *Chemical Research, Development, and Engineering Center, U.S. Army, Aberdeen Proving Ground, Maryland 21010-5423.* (Present address DAB: *Dept. Forestry, Wildlife and Fisheries, Univ. of Tennessee, Box 1071, Knoxville, Tennessee 37901-1071.* Present address TJM: *U.S. Forest Service, Ouachita National Forest, Hot Springs, Arkansas 71902.*) *Received 30 July 1991, accepted 1 Feb. 1992.*

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Annual variation in the timing of breeding of the Monk Parakeet in relation to climatic factors.—The timing of breeding of a species is regarded as adaptive. According to Lack (1950), natural selection normally favors those individuals rearing offspring during the season that maximizes productivity and/or minimizes mortality.

Most birds have evolved a hereditary response to environmental changes (proximate factors, sensu Baker 1938) that predicts the favorable season well in advance. The variation in day length, at middle and high latitudes, is the primary signal to induce the basic physiological and behavioral preparations for breeding (Lack 1950, Immelmann 1971, Murton and Westwood 1977). However, additional factors are generally required to adjust the onset of egg laying to slight variations in ecological conditions (Immelmann 1971).

The Monk Parakeet (*Myiopsitta monachus*) has a breeding season restricted to spring and summer. The mean date of onset of laying has been found to vary among years within a 19-day range from late October to mid November (Navarro et al., unpubl. data). The regularity in timing of breeding suggests that the increasing day-length may be the basic environmental cue controlling this species' breeding season. However, the year-to-year variation indicates that other factors also may influence the onset of breeding in the Monk Parakeet.

This paper is focused on the role of proximate factors (other than photoperiod) that may induce slight annual shifts in the timing of breeding in the Monk Parakeet. We used correlation analysis to investigate the potential effects of rainfall and temperature on the date of initiation of egg laying.

Study area and methods.—The information presented here was collected during a long-term study of the breeding biology of the Monk Parakeet, conducted in a 610-ha area located

close to the town of Jesús María in Córdoba Province, Argentina. Detailed descriptions of the study area and procedures of data collection are presented in Navarro et al. (1992).

During six years (1983 to 1988), we inspected all accessible Monk Parakeet nests in the study area at 7- to 12-day intervals, from the pre-laying period in October to early the end of the breeding season in March. The dates of laying refer below to first clutches only (i.e., females laying their first egg of the season). The beginning of laying was estimated for each clutch by back-dating, based on the average interval between successive eggs and the average incubation period (2.2 and 24 days, respectively) for this species (Navarro 1989). The age of nestlings, calculated by a growth curve equation (Navarro and Bucher 1990), was also used for back-dating when necessary. We excluded from the analysis all clutches in which no accurate laying date could be estimated. Climatic data were recorded at the Córdoba airport 26 km south of the study area. Average mean, maximum, and minimum daily temperatures, rainfall, and number of rainy days and those with heavy rain (≥5 mm) were calculated for periods of different ending dates and length.

We used the two correlation techniques applied by Slagsvold (1976) to detect those periods during winter and spring that showed the strongest correlations between climatic data and dates of clutch initiation: (1) By varying the length of the analyzed period, with every one ending on the same fixed date. The periods tested were increments of five days between 10 and 100 days before the fixed ending date, respectively. The terminal date (1 November) was established as four days before the overall average date of onset of laying in the population (Navarro et al. 1992). The four-day interval represents an estimate of the time required to produce an egg; this interval was not available for the Monk Parakeet and was taken from other bird species (Slagsvold 1976, Orell and Ojanen 1983), and (2) By varying the ending date of the analyzed period using a certain period length. We analyzed every interval of a length mentioned in (1) successively, throughout the 100-day interval before 1 November.

Results.—On average, 26 first-clutches (range 14–32) were used to calculate the mean laying date of each year. The daily maximum temperature showed the highest significant negative correlation with the mean date of onset of egg laying (i.e., an advance in the time of breeding is associated with higher temperatures). When the mean laying dates were compared with the average daily maximum temperature recorded during periods of varying length, each ending on 1 November (method A), the period providing the highest significant correlation ($r = -0.962$; $N = 6$; $P < 0.01$) was 50 days, from 13 September onwards (Fig. 1). Method B gave the strongest significant correlation for the average of daily maximum temperatures in the 55-day period between 31 August and 24 October ($r = -0.996$; $N = 6$; $P < 0.01$). Averages of daily maximum temperatures during this period ranged from 23.0 to 24.2°C.

Rainfall showed a non-significant correlation with egg-laying dates, based on method A (Fig. 1). However, number of rainy days resulted in significant positive correlations by method B, the highest ($r = 0.864$; $N = 6$; $P < 0.05$) being for the 40-day period between 17 September and 26 October. Moreover, when only days with heavy rains (≥5 mm) were considered, there was a closer correlation for the 35-day interval between 2 September and 6 October ($r = 0.926$; $N = 6$; $P < 0.01$).

In a further step, we tried to partial out the effect of temperature on the relationship between days with heavy rains and average date of beginning of egg laying. We calculated partial correlation coefficients between average date of start of egg laying and the two climatic variables: number of days with heavy rains (from 2 September to 6 October) and average of daily maximum temperatures (31 August to 24 October). The temperature showed a significant negative correlation with date of start of breeding when the number of days of heavy rains was held constant ($r = -0.970$; $N = 6$; $P < 0.01$). On the other hand, for a

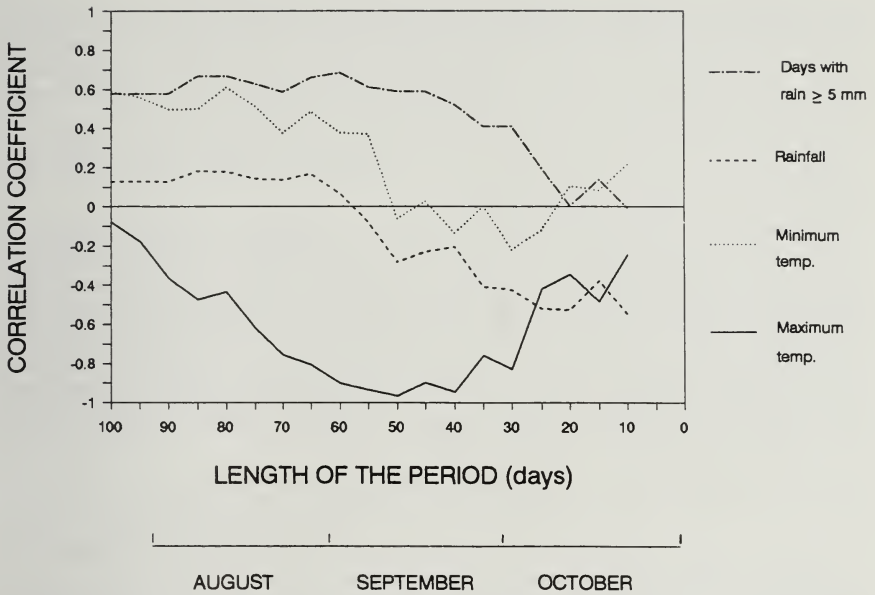

FIG. 1. Variation in the correlation coefficient obtained for the relationship between date of start of egg laying in Monk Parakeets and climatic factors occurred during periods of different length ending on a fixed date (1 November). Notice that a negative correlation means that earlier breeding attempts are associated with higher values of the climatic factor.

fixed maximum temperature, number of days with heavy rains and date of start of breeding were not significantly correlated ($r = 0.244$; $N = 6$; $P > 0.05$).

Discussion.—Higher maximum temperatures experienced in late-winter to mid-spring are correlated strongly with earlier breeding in the Monk Parakeet. Therefore, although the regularity in the timing of breeding suggests that photoperiod may be the principal factor setting the breeding season in Monk Parakeets, maximum temperatures also may exert some influence. In contrast with the results obtained by Lofts and Murton (1966) in the Wood-Pigeon (*Columba palumbus*), a sharp rise in temperature seems not to advance egg laying in the Monk Parakeet, as the period in which this species is sensitive to that climatic factor is of considerable length.

The influence of temperature on the initiation of laying has been well documented in Eurasian tits (*Parus* spp.), in which breeding begins earlier during mild springs than during cold ones (Perrins 1965, 1973; Slagsvold 1976; Murton and Westwood 1977; O'Connor 1978; Orell 1983; Orell and Ojanen 1983).

The opposite results obtained from linear and partial correlation analysis between rainy days and date of breeding suggest that rainy days seem to produce only an indirect influence on the date of onset of breeding. Therefore, the apparent relationship between these variables could well be due to chance or to lower temperatures caused either by the lack of sunshine or by the rain, and not to a direct hindering of the courtship and nest-reconditioning behavior or foraging activities.

Although average maximum temperatures of above 23°C seem to work as a secondary factor that advances breeding in Monk Parakeets, the relationship between temperature and

the onset of laying is probably complex. As earlier breeders have a higher breeding success within the population (Navarro and Bucher, unpubl. data), many pairs would presumably raise more young if they could begin egg laying earlier than they do. Females may produce their eggs when another limiting factor (possibly food supply) allows. In the absence of data on the association between climate and food resources for Monk Parakeets, it is not easy to establish if the onset of egg laying results from the direct effect of the preceding temperature, by a linked factor such as an improvement in the availability or quality of food, or via some modification in the aspect of the landscape.

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Joaquín L. Navarro and Enrique H. Bucher, *Centro de Zoología Aplicada, Universidad Nacional de Córdoba, casilla de correo 122, 5000 Córdoba, Argentina.* *Received 1 Aug. 1991, accepted 23 Jan. 1992.*

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Capsaicin effects on consumption of food by Cedar Waxwings and House Finches.—Capsaicinoids (e.g., N-vanillyl-n-nonamide, norcapsaicin, nordihydrocapsaicin, capsaicin, dihydrocapsaicin, homocapsaicin, homodihydrocapsaicin; Hoffman 1983) are aromatic amides and the pungent principles in Capsicum peppers. Although these substances are strong chemical irritants for most mammals (e.g., Rozin et al. 1979), the available data suggest that they are inoffensive to some birds. For example, European Starlings (*Sturnus vulgaris*) and Rock Doves (*Columba livia*) are unresponsive to these compounds, even when concentrations greatly exceed those which mammals avoid (Szolcsanyi et al. 1986; Mason et al., in press).

The present studies were designed to explore further the apparent taxonomic specificity of capsaicin. We also measured the capsaicin levels present in wild fruits and used that concentration in our behavioral tests.

Materials and methods.—To determine an ecologically valid concentration of capsaicin to use in behavioral tests, we determined the average amount of capsaicin present in wild peppers (*Capsicum annuum*). Fruits were collected during the summers of 1990 and 1991 at the Audubon Sabal Palm Sanctuary, Cameron County, Texas. Fresh specimens were frozen immediately and shipped to the Monell Chemical Senses Center, Philadelphia, Pennsylvania. Upon arrival, capsaicin concentrations were determined according to the method of Hoffman et al. (1983). Fruits were weighed, ground to a paste, and extracted with 95% ethanol at 65–75°C for five h. Suspended material was allowed to settle, and the supernatant was transferred to Teflon-lined screw-capped vials. Samples of fluid (50 μl) were injected into a Waters Associates ALC/GPC high performance liquid chromatograph (HPLC) system with a 10 μl Bondapak C_{18} column and a guard column of Bondapak C_{18}/Corasil (Waters Associates) with detection at 280 nm (Hoffman et al. 1983).

Five male Cedar Waxwings (*Bombycilla cedrorum*) were mist-netted near Gainesville, Florida, and shipped by air to the Monell Center. Five male House Finches (*Carpodacus mexicanus*) were funnel trapped in the Philadelphia area. All birds were caged individually (dimensions: 61 cm × 36 cm × 41 cm) under a 12:12 light-dark cycle (lights on 07:00–19:00 h EST).

During a two-week period of adaptation to captivity, canary-finch feed (AVN®, Purina Mills, Inc., St. Louis, Mo.; hereafter referred to as feed) and tapwater were provided ad libitum. Because waxwings are frugivorous, their diet was supplemented with mashed bananas and blueberries every third day.

A five day pretreatment period immediately followed adaptation. On each pretreatment day, birds were food deprived overnight (18:00–08:00 h). Between 08:30 and 09:00 h, one cup containing 20 g of control feed was placed in each cage. Control feed samples were prepared by spraying plain feed with diethyl ether 24 h before testing, and then placing the feed under a fume hood to evaporate the ether (Jakubas et al. 1991). Consumption, spillage, body mass, and dry feces mass for each bird were measured at the end of each test. After testing and until lights out, all birds were provided free access to plain feed and tapwater.

A five-day treatment period immediately followed pretreatment. During treatment, birds

were given feed containing 1000 ppm capsaicin in three h tests. To prepare the capsaicin-treated feed, samples were sprayed with reagent grade synthetic capsaicin (Aldrich Chemical Company, St. Louis, Mo.) dissolved in diethyl ether (Aldrich Chemical Company, St. Louis, Mo.). As in pretreatment, the treated feed samples were placed under a fume hood for 24 h to evaporate the ether prior to testing. Consumption, spillage, body masses, and feces dry masses were recorded, as described above. Body masses and dry feces masses were recorded as gross measures of health during the experiment.

Consumption, body masses, and dry feces masses were evaluated separately in three factor analyses of variance (ANOVAs) with repeated measures over periods and days. The independent factor in these analyses was species. Tukey post-hoc tests (Winer 1971:198) were used to isolate significant differences among means ($P < 0.05$).

Results.—Chromatography showed that the average capsaicin concentration in wild fruits was 1000 ppm (SE = 10.5 ppm). Consumption of treated feed by Cedar Waxwings was greater than that of House Finches, although it was slightly, albeit significantly, depressed on treatment day 1 ($F = 28.3$; df = 1,4; $P < 0.007$). Consumption by House Finches remained constant between periods.

When body masses were examined, there were no biologically significant treatment effects. Cedar Waxwings were heavier than House Finches ($F = 50.0$; df = 1,4; $P < 0.003$). Analysis of feces dry mass showed that the mean mass of Cedar Waxwing feces was greater than the mean mass of House Finch feces ($F = 256.8$; df = 1,4; $P < 0.0005$). Otherwise, there were no biologically significant treatment effects.

Discussion.—Wild capsicum peppers contain approximately 1000 ppm of capsaicin. This concentration is repellent to house mice (*Mus musculus*), deer mice (*Peromyscus maniculatus*), and Norway rats (*Rattus norvegicus*) (J. R. Mason, unpubl. data), but does not substantially affect feeding by Cedar Waxwings (present experiment), House Finches (present experiment), Rock Doves (Szolcsanyi et al. 1986), or European Starlings (Mason et al., in press). Although the reasons underlying the apparent taxon-specific aversiveness of capsaicin remain obscure, anecdotal evidence suggests one intriguing possibility. We speculate that the differential sensory effects of capsaicin on mammals and birds may reflect a selected response related to the reproductive strategy of Capsicum plants. Specifically, capsaicinoids may exploit the separately evolved sensory systems of the two taxa (Mason et al., in press) and selectively repel mammalian seed predators but not avian seed dispersers. These irritant chemicals are present only in the red, upright fruit, and occur nowhere else in Capsicum plants. The fruits themselves are high in vitamins, protein, and lipids (Herrera 1987), traits which are correlated with avian dispersal (Willson and Thompson 1982, Willson and Hoppes 1986). Birds are commonly seen feeding on wild capsicum fruits, colloquially known as 'bird peppers' (R. Smith, pers. comm.). Rodents have not been observed eating these fruits, although they will readily consume Capsicum seeds in the absence of capsaicinoids (D. Norman, unpubl. obs.). Whether or not the function of capsaicin is similar to that which we propose remains to be determined, but the hypothesis is readily testable.

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Donald M. Norman, *Dept. of Biology, Univ. of Pennsylvania, Philadelphia, Pennsylvania 19104*; J. Russell Mason and Larry Clark, *USDA/APHIS/S&T, Denver Wildlife Research Center and Dept. of Biology, Univ. of Pennsylvania, % Monell Chemical Senses Center, 3500 Market Street, Philadelphia, Pennsylvania 19104.* *Received 3 Dec. 1991, accepted 27 Jan. 1992.*

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First description of the nest and eggs of the Black Solitaire.—The Black Solitaire (*Entomodestes coracinus*), a little-known species whose nesting has not heretofore been described, occurs only in upper tropical and subtropical forests along the Pacific slope from the headwaters of the Río San Juan in W-C Colombia to NW Ecuador (Meyer de Schauensee 1970, Hilty and Brown 1986). It is fairly common at La Planada Natural Reserve, Dpto. de Nariño, Colombia (1°15′N, 78°15′W), where I discovered two active nests, each of which held two eggs.

I found the first nest on 19 July 1990, along the crest of a ridge at ca 1900 m when an adult was flushed from the nest and reappeared less than 5 min later. The open cup nest was anchored to several vertical stems of an aroid (*Monstera*) attached to the trunk of a melastome tree (*Conostegia* sp., ca 16 cm dbh and 6 m in height), leaning out from the trunk 1.7 m above the ground. Canopy height in the nest-site was ca 20 m. The nest was comprised mostly of fresh moss, with an inner lining of brownish rootlets. The nest cup was 48 mm deep and 90 mm wide (inside diameter). The subelliptical eggs were light glossy green with fine, brown, randomly distributed spots. Two days later, I again flushed an adult from the nest; this bird reappeared nearby on at least four occasions in the next 25 min. Voucher photographs of this nest with eggs and its habitat have been deposited in VIREO (V06-8-001, V06-8-002).

On 21 July 1990, I found a second nest of similar construction, approximately 1 km to the NW. It was located on a tree fern (*Cyathea* sp., ca 8.8 cm dbh and 3.5 m in height). The tree fern was densely covered by bromeliads (*Guzmania* sp.), aroids (*Anthurium* sp.), and small ferns. I found this nest on a trail at ca 1700 m. Both nest sites were in deep shade under a closed canopy. The shape, color, and markings of the eggs were similar to those described for the first nest, except that they were finely specked with brown at the smaller end, with the spotting becoming heavier and blotched at the larger end, rather than randomly speckled. The average measurements and weight of the four eggs were 27.6 ± 0.4 mm × 19.3 ± 0.6 mm and 4.9 ± 0.4 g, respectively. On 7 August both nests were empty and the adults were not seen. The eggs in the first nest, and possibly an adult bird, were lost to predation between 23 July and 7 August, because I found numerous small body feathers scattered around the nest. The fate of the eggs in the second nest is unknown.

The nest of the Black Solitaire resembles those described for the Black-faced Solitaire (*Myadestes melanops*) (Skutch 1972, Stiles and Skutch 1989) and the Andean Solitaire (*M. ralloides*) (Miller 1963, Wallace 1965), which are bulky open cups composed largely of mosses, lined with dark fibrous rootlets and similar materials. The eggs differ from those of Myadestes in their greenish ground color and sparser spotting which is less concentrated toward the thick end.

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William Beltrán, *Sociedad Vallecaucana de Ornitología, A. A. 26538, Cali, Colombia.* *Received 1 June 1991, accepted 15 Dec. 1991.*

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American Coot kills Yellow-headed Blackbird nestlings.—I know of only one witnessed predation event by an American Coot (*Fulica americana*) on a vertebrate—a nestling Red-winged Blackbirds (*Agelaius phoeniceus*) (pers. comm. cited in Burger, Auk 85:449–451, 1973). While making observations at the Creston Valley Wildlife Management Area in

Creston, British Columbia, I witnessed coot predation of Yellow-headed Blackbird (*Xanthrocephalus xanthrocephalus*) nestlings. The observations were made from a blind 130 m from a bullrush clump containing a monitored coot nest.

At 12:40 on 29 May 1991, I observed an adult coot repeatedly shaking, dropping, and retrieving something in its beak. These behaviors lasted for a few minutes until the coot lowered its head to the "Charge" posture (Gullion, Wilson Bull. 64:83–97, 1952) and very slowly paddled into a bullrush clump. It approached the bullrushes from the side opposite to an active coot nest (P4N41, presumably its own) and was moving much more slowly than when the Charge display is used in aggressive interactions. It reappeared a second later in a rushing flap, closely followed by a pair of Yellow-headed Blackbirds. The blackbirds physically attacked the coot until it was a meter or two from the bullrushes. The coot made five or more forays into the bullrushes, returning either in a flap, with the blackbirds in pursuit, or resurfacing from a dive. These forays were separated by short bouts of sitting in the water facing the clump, occasionally preening or picking at the object. Finally the coot emerged with a beak full of brown cattail leaves, which it dropped to the water. The only cattail leaves in the bullrush clumps were the nests of Yellow-headed Blackbirds. I then began to approach the scene by canoe; two or three more coot forays into the clump occurred before the birds were frightened off. At the site, I discovered an empty, tipped-over, Yellow-headed Blackbird nest about 30 cm from the water surface where the coot had been entering the clump. A brief search of the area where the coot had been sitting revealed the remains of two blackbird chicks, one almost whole but mangled and the other little more than a single leg. These remains were the only obvious objects I could find that the coot could have been shaking. Tarsal lengths and general appearance indicated that the nestlings were about five days old.

While the evidence is circumstantial, three points lead me to believe that this was a predation event and not scavenging. First, the coot deliberately tore the nest apart and there was no other source of cattail leaves. Second, the parental defense was active and physical (pecking and clawing at the coot), suggesting that the nestlings were very recently removed from the nest. Third, the coot was clearly tearing up and eating the nestlings, which were recently killed when I found them.

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Peter L. Hurd, *Behav. Ecol. Res. Group., Dept. Biol. Sci., Simon Fraser Univ., Burnaby, British Columbia, Canada, V5A 1S6.* *Received 22 Oct. 1991, accepted 1 Jan. 1992.*

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ORNITHOLOGICAL LITERATURE

DISTRIBUTION AND TAXONOMY OF BIRDS OF THE WORLD. By Charles G. Sibley and Burt L. Monroe, Jr. Yale Univ. Press, New Haven, Connecticut, and London, England. 1990: xxiv + 1111 pp., 25 pp. unnumbered maps. $125.00.—At the outset, the authors present their five goals in preparing this massive work: "(1) to delineate the present distribution of the species of birds of the world in moderate detail and up-to-date to the beginning of 1990; (2) to arrange species in a classification based primarily on evidence of phylogenetic relationships from the comparisons of their DNAs; (3) to provide a numbering system for the species of living birds; (4) to include a gazetteer with maps indicating the positions of localities mentioned in the distributional accounts; and (5) to provide an index to scientific and English names of species."

The first goal is admirably achieved. Each entry consists of the scientific name, describer's name, date of description, English name, world number, a brief description of the habitats and elevations in which the bird is found, geographic range, and where appropriate, alternate names. A list of 46 errata is included. More will certainly be found, but this is a modest number for a work of this size and complexity.

The total number of the world's species of birds may never be determined because of the blurred line between species and subspecies. The 9672 "biological" species treated in this work are more than generally are recognized, but erring in this direction is better than the reverse. In a time like this, when there is a trend away from "lumping" toward recognizing species formerly considered subspecies, there is a distinct advantage in having separate data sets for infraspecific taxa that might be raised to the specific rank in the future.

The index to the scientific and English names of the species covers 171 three-column pages and is vital to finding a species in what to almost everyone is a new sequence. It will also be useful to those who know only the scientific or English name of a species.

Furthermore, a gazetteer and maps can prove useful, especially in times when geographic names are in a state of flux. The maps, however, leave something to be desired. The lines on many are too fine and the lettering so bold as to make the geographic divisions even more difficult to follow. On the map of North America, the names of the United States appear, but the lines between states are omitted. This may well confuse those unfamiliar with the geography of our country.

What is most controversial is the sequence in which the species are presented. This is based on the phylogeny and classification of birds by Sibley, Ahlquist, and Monroe (Auk 105:409–423, 1988). This in turn is based on studies, primarily by Sibley and Ahlquist, on the DNA-DNA hybridization data from 1700 species, representing all but a few of the major groups of birds. These studies are a major advance in providing a phylogeny of birds based on data from a molecular system that can provide not only evidence for the sequence of branching in the family tree of birds but also an estimate of when each branching occurred. (The latter assumes an equal rate of DNA sequence divergence across taxa, which is controversial.) Therefore, in spite of its controversial nature, it gives us the most complete series of hypotheses to date for reconstructing the evolution of birds.

It has long been recognized that phylogenetic hypotheses can be strengthened by congruent patterns from different lines of evidence. In many instances, such patterns have also been provided by Sibley and Ahlquist in their publications. Thus, the phylogeny has been based on a tremendous amount of new data to which has been added a formidable review of the available information on the subject. Nevertheless, no phylogeny can be taken as carved in stone. Newer, more powerful molecular techniques have been developed in the sixteen years

since Sibley and Ahlquist settled on their technique for DNA-DNA hybridization, and the amino-acid sequences of molecules have been shown to be subject to convergent or parallel evolution much as are morphological structures. Because DNA-DNA hybridization by its nature is a phenetic method providing information on the amount but not the direction, of genetic change, some claim it is an inappropriate method of constructing phylogenies. It also appears that DNA-DNA hybridization may not be the most accurate molecular method for this purpose (see Hillis and Moritz [eds.] 1990. "Molecular systematics: context and controversy. Sinauer Assoc. Inc., Sunderland, Massachusetts, and Springer and Krajewski. 1989. Quart. Rev. Biol. 64(3):291–318 for critiques of this technique and comparisons of it with other molecular ones.) Finally, the methods used by Sibley and Ahlquist in analyzing their data have been questioned (Gill and Sheldon, 1991, Science 252:1003–1005), and several recent studies have provided evidence against the branching pattern of parts of the tree.

While the work presents well documented advances in both the phylogeny and classification of birds, it also presents phylogenetic hypotheses and classifications that are not well supported. This is especially true at the higher levels of the classification, where the DNA evidence is weak. Traditionalists will find particularly disturbing the expansion of the Ciconiiformes to include what were formerly the Charadriiformes, sandgrouse, diurnal birds of prey, grebes, Pelecaniformes (variously broken up), penguins, loons, and petrels. The breaking up of the pelecaniform birds can be questioned on strong morphological grounds. There are several places where groups (e.g., the grebes) are placed within specific groups without strong evidence, instead of being labelled "*incertae sedis.*" Many non-systematists will accept these placements as gospel and will question the desirability of conducting further systematic research where, in fact, much is needed.

With new up-to-date studies we can hope to keep extending our understanding of the phylogeny of birds, but making a linear classification from even a perfect tree is another complex matter. It takes 9671 branchings to produce a tree of 9672 twigs. To place these twigs in a linear sequence requires a decision at each branching point as to which branch to put first and which second. A set of guidelines is needed to make these decisions repeatable. Such guidelines have been proposed, but, unfortunately, none have been formally accepted and used uniformly by ornithologists. If we are to approach a stable linear classification, some action on this is needed.

The method of sequencing taxonomic groups used in this work is not clearly stated, except that the branchings were treated in the order of the estimated time they occurred, and the ramifications of each branch are followed to the end before going back to the second branch. This is the only logical choice, but how to determine which of any two branches to list first is unclear. Where DNA-DNA hybridization and/or other new data were available, new arrangements were made. Many of these are at the level of the family or higher or are on groups which had been studied by Sibley and Ahlquist. The remaining 80+% of the branching sequences, most of them at the genus or species level, were taken from other works, primarily Peters' "Check-list of Birds of the World." Most, if not all, of the contributions to the latter work, including mine, used subjective criteria from "advanced" or "specialized" characters in arranging sequences. Thus, it is inevitable that as research on the phylogeny of birds continues and a set of criteria for sequencing phylogenies is formally established and followed, we can expect to see continued changes in our classification.

The numbering system proposed in this work was expanded from that long in use in the AOU check-lists of North American birds, and that has not been altered with changes in the systematics of these birds since its inauguration. Birds not found in the original AOU check-list area have been given numbers, the first digit of which corresponds to the major geographic region in which the birds are found. We are thus presented with a hybrid system,

geographic as well as taxonomic. North Americans may be glad that the numbers of their birds can remain constant through further changes in classification, although others may label the numbering system parochial and may object to its dual basis.

While much of the phylogeny in this work is probably valid, much of it may well prove wrong, and the Sibley-Ahlquist-Monroe classification has resulted in much controversy, some of it acrimonious. In matters of taxonomic change, I confess to a conservative attitude based on the fact that an incorrect change requires another change to remedy it. I am therefore against changes based on a single line of evidence unless there is strong corroborative information. If we take this conservative approach and if we adopt an objective code for sequencing phylogenies, when the dust settles on the controversy, we should have a classification that in the end will require relatively few changes. In the meanwhile, we can use this book as a most valuable source of information on the distribution and habitats of the world's birds and as a stimulus for further studies on their phylogeny.—Robert W. Storer.

A Complete Checklist of the Birds of the World. (Second Edition). By Richard Howard and Alick Moore. Academic Press, London. 1991:xxxiv + 622 pp. $49.50.—Since the original edition of this world list appeared in 1980 (reviewed in *The Wilson Bulletin,* 93:437, 1981) the final two volumes of the Peters Checklist and the Sixth Edition of the A.O.U. Checklist, as well as some other important works have been published. This new version appears to make use of such material through 1988.

The result is a convenient, well-produced list of more than 9200 species. This is the only world list that treats subspecies. These are all listed, together with very abbreviated statements about their ranges. An English name is given for each species which, unfortunately, in many cases will differ from the names that will result from the program initiated at the recent I.O.C. meeting to compile an agreed-upon list of such names.

For each of the recognized families, a list of publications on the taxonomy of the family is given. This makes a convenient resume of recent taxonomic literature. Another strong point is the inclusion of very thorough indices of both scientific and English names, making it easy to look up a desired species.

As in the earlier version the classification used is that of the Peters "Checklist of the Birds of the World." This arrangement may now be obsolete with the publication of the totally different classification proposed by Sibley, Ahlquist, and Monroe (1990) (see review elsewhere in this issue). The authors recognize this and remark, "This may therefore be one of the last opportunities to produce an up-to-date usable list which bears some relationship to the historical order and form of traditional checklists, that is to say a list we can use because we know where to look and what to look for."—George A. Hall.

The Birds of Japan. By Mark A. Brazil, illus. by Masayuki Yabuuchi. Smithsonian Institution Press, Washington, D.C. 1991:466 pp., 6 color plates, 65 numbered text figs., 578 range maps. $49.95.—Publications on Japanese natural history abound, but most are in Japanese, their contents not intelligible to most foreigners. In recent years, such books written in English have brought the rich biota of these islands to the attention of more and more biologists, both professional and amateur. The present book fills a need for information about the distribution and occurrence of Japanese birds, a rapidly expanding area of knowledge.

Unlike many regional bird books, this one makes no attempt to be a field guide. Instead, the author concentrates on occurrence and aspects of the biology of each species. The species

accounts include very detailed summaries of distribution and seasonal status; a description of preferred habitats (including seasonal changes); a brief account of breeding biology (breeding season, nest location, clutch size, and incubation period) for breeding species; a description of vocalizations; an account of subspecies recorded from Japan; and occurrence by island, often with a chronology of known records. The accounts of Japanese endemics average longer than those of widespread species, presumably by design.

There is also a brief introduction to Japan's climate and habitats, its avifauna, its ornithological history, and birdwatching in the country. The climate descriptions are particularly interesting, as is the description of changing (and not-so-changing) attitudes toward Japanese wildlife. There is even a list of 43 "anticipated species," mostly migratory species that occur to the northeast or northwest of Japan. The bibliography of over 1300 titles (cited by number in the text) is astonishing because only a tiny proportion of them are in Japanese; this list presents a monumental record of the author's diligence. I am not qualified to comment on its accuracy or thoroughness, both important in a regional survey, but the abundance of detail promotes confidence.

Each of the 583 species recorded from Japan is listed with its current status. Occurrence throughout the archipelago is summarized, not an easy matter, as few species have the same status from one end to the other. Only 52 (33%) of 158 native land-bird species that breed in Japan breed throughout the main islands, and only 14 of these species (9% of the total) occur through all or most of the southern archipelago. No generalities emerge from this assessment other than that a high proportion of the most widely distributed breeders are resident. That list includes widespread species such as Common Kingfisher (*Alcedo atthis*) and Great Tit (*Parus major*) and narrow endemics such as Japanese Pigmy Woodpecker (*Dendrocopos kizuki*) and Varied Tit (*P. varius*).

Students of avian biogeography will find much of interest in this book, as no fewer than 12 biogeographic boundary lines are associated with Japan (p. 8). Distribution boundaries tend to be within rather than between the main islands, probably corresponding to habitat boundaries, but the Soya Strait between Sakhalin and Hokkaido has been a major gap. Thirty-three land and freshwater species breed on southern Sakhalin but not Hokkaido and 28 on northern Hokkaido but not Sakhalin. The islands are similar in size and habitat and less than 40 kilometers apart, yet there is a substantial avian disjunction between them.

Because it lies along a coast and extends through many latitudes, Japan has a substantial list of rare and casual visitors. Most, of course, come from the Asian mainland, but, surprisingly, many visitors from North America have been recorded. These include seven species of waterfowl, Sandhill Crane (*Grus canadensis*), 11 shorebirds (including Lesser Golden-Plover [*Pluvialis dominica dominica*]), three gulls (including Franklin's Gull [*Larus pipixcan*] and Thayer's Gull [*L. thayeri*]), and, more surprisingly, four emberizine sparrows (with numerous records of both Savannah Sparrow [*Passerculus sandwichensis*] and White-crowned Sparrow [*Zonotrichia leucophrys*]).

Records of rare species are plotted individually on the maps, an excellent feature although probably indicating the distribution of ornithologists and birdwatchers at least as much as the distribution of rare birds; the Tokyo area and Okinawa are the sites of many such records.

The diversity of the Japanese avifauna is a consequence of two factors that influence diversity in opposite directions. First, it is an island nation, with reduced diversity compared with the mainland. Second, although it is a small country, smaller than California, it extends over 25° of latitude, slightly more than the lower 48 states. The series of large and small islands stretches from Hokkaido, with strong elements of the Russian taiga, to the southernmost Nansei Islands, almost tropical. The country is rich in birdlife, considering that it has been highly disturbed for a long time. Perhaps this disturbance accounts for what seemed to me a surprising scarcity of birds, both species and individuals, on several brief visits to

Japan. Is this because of long inhabitation by humans, or are there other, more interesting, ecological factors?

Other tidbits that can be gleaned from this book include the long isolation of Japan from the mainland and from other islands such as Taiwan and Sakhalin, as indicated by its many endemic species (including 7 seabirds) and subspecies; hopeful reports of the slow recovery of Short-tailed Albatross (*Diomedea albatrus*) and Japanese Crane (*Grus japonensis*) populations; the distinct host preferences of the four species of *Cuculus* breeding in Japan; the confusion surrounding the names of Japanese (*Erithacus akahige*) and Ryu Kyu (*E. komadori*) robins; the documentation of the spread of the European Starling (*Sturnus vulgaris*) into Japan from the west (one might say it now occurs from Seattle to Tokyo) as well as the first occurrence and breeding of the House Sparrow (*Passer domesticus*) in 1990; and the fact that this very advanced country still allows thousands of passerines to be caught in mist nets and sold to be grilled.

The color plates and black-and-white text drawings are superb, and I could only regret that the same artist could not have been employed to produce both beautiful and *accurate* paintings for the Wild Bird Society of Japan's 1982 field guide. Fortunately, a great number of eastern Asian endemics are illustrated by Yabuuchi.

What else might have been included but wasn't? A brief statement of the overall geographic range of each species would have placed its occurrence in Japan in context. Also, it is not obvious why vocalizations were not described for some species, even breeding ones. There would have been much for an avian ecologist here if the author could have presented means as well as ranges for such variables as clutch size, nest height, perching height, and habitat preference. Also, a concise summary of food habits (included for some species) would have rounded out the wealth of biological information presented. However, these additions would have necessitated considerably more effort on the part of the author, and the amount of effort put into this book has been prodigious in any event. Otherwise, the book fulfills its obligations well.

The author has done more than anyone else to promote the visitation of Japan by foreigners interested in birds, having written three books on bird finding in Japan and now this very useful book. Perhaps the most interesting message of the book, to me, was that it is written for birdwatchers rather than ornithologists. The introduction makes this clear, and I see that scholarly books such as regional avifaunas will be increasingly intended for the large number of amateurs rather than for the professionals for whom such books were written in the past. This shows, as much as anything I have seen, the extraordinary significance of amateurs to ornithology.—Dennis R. Paulson.

Annotated Checklist of the Birds of Ontario, Second edition, revised and expanded. By Ross D. James. Royal Ontario Museum, Toronto, Life Sciences Miscellaneous Publications, 1991:128 pp., 2 figs., $13.95.—Fifteen years after the first edition of a book bearing this title, one of the original authors has undertaken a much needed updating. In doing so, he has drawn thoroughly on the extensive literature on Ontario bird distribution that has accumulated in the intervening years. The book is unquestionably the most complete attempt at listing the birds of Ontario. It is unlikely that any published records have been overlooked, and I know of very few unpublished records that have escaped the author's attention.

The book is organized with an introduction, a checklist of species comprising the bulk of the text, and appendices dealing with probable escapees and subspecific variation, providing enough detail for the scope of such a book. Within each species listing, there is information on its breeding status, its distribution frequency and relative abundance, all on a season-by-season basis, its dates of occurrence in the province, egg dates when appropriate, and,

where the distinctions are obvious, some details of subspecies found in Ontario. Published records of rarities are cited, and the nature of the documentation of unpublished records of rarities is described in many cases.

While the completeness of the listing is exceptional, it is regrettable that, probably because of space constraints, many of the records referred to, especially in the case of vagrants, are lacking in details. One is left to wonder about the summer records of Harlequin Duck (*Histrionicus histrionicus*) and Barrow's Goldeneye (*Bucephala islandica*), for example, the latter in "the south," which is a vast area larger than several states in the U.S.A. Similarly, it would be interesting to have a little more information about the scattered records of American Swallow-tailed Kites (*Elanoides forficatus*), spring and summer Sabine's Gulls (*Xema sabini*), Lark Bunting (*Calamospiza melanocorys*) at James Bay, and Rosy Finch (*Leucosticte arctoa*) on Manitoulin Island, for example.

The author systematically uses a standard terminology in describing the relative abundance, season by season, of the species listed. In applying the terminology, however, he necessarily relies on his own field experience, which in a few cases differs from my own. As an example, in his experience the Magnolia Warbler (*Dendroica magnolia*) is an "abundant" migrant, meaning that more than 500 could be seen in a day, whereas the Yellow-rumped Warbler (*D. coronata*) is, except locally, described as a "common" migrant, meaning that the numbers seen in a day are seldom more than 500. In my experience, the relative abundance of these two species is the reverse.

Technically, the book is almost flawless. To find only one minor typographical error in 85 pages of text and an additional 43 pages of acknowledgements, appendices, references, and index is a rare treat. Any ornithologist or birder with a serious interest in Ontario bird distributions will want to have this inexpensive reference book on his/her shelf.—Frederick M. Helleiner.

The Birds of British Columbia. By R. Wayne Campbell, Neil K. Dawe, Ian McTaggart-Cowan, John M. Cooper, Gary W. Kaiser, and Michael C. E. McNall. Mitchell Press, Vancouver, British Columbia, Canada. 1990: Volume 1, 514 pp., 1 color plate, 71 range maps, 340 numbered figs. and black-and-white photographs, and 17 tables. Nonpasserines, Introduction, Loons through Waterfowl. Volume 2, 636 pp., 153 range maps, 324 figs. and photographs, and 19 tables. Nonpasserines, Diurnal Birds of Prey through Woodpeckers. $99.00.—After years of rumors that a book on the birds of British Columbia was being written, followed by years of more positive rumors, made still more real by tales of woe and extended deadlines, the long-awaited, up-to-date treatise on the B.C. avifauna has finally appeared (19 years after conception) in two large volumes. Another volume (I suspect this will become two volumes, just to add to the new rumors) is alleged to be in the works. What I have in front of me is quite different from any other provincial or state bird book I know. Solid data, presented in a crisp, organized manner, form the bases of these volumes. I like them.

Volume 1 starts with a general introduction covering 150 pp., subdivided into three sections. The first of these (11 pp.) deals with the national and international importance of British Columbia as a region for birds, the history of how the two volumes came to be, and how the subject matter is organized. The data base is impressive. Under the able baton of maestro R. Wayne Campbell, some 4600 enthusiasts of all stripes collected the field data, consisting of more than 150,000 records of nests and their contents and an additional 900,000 distribution records on nonpasserines alone. In a way these volumes are a well deserved salute to the members of the orchestra.

The second section (39 pp.) of the introduction deals with the ornithological history of British Columbia, from the earliest explorer, William Anderson, James Cook's official nat-

uralist, to present day naturalists, researchers, conservationists, and managers, with photographs of many of them. The photographs clearly show the historical shift from the shotgun, so important in the early days, to binoculars.

The third and last section (97 pp.) of the introduction deals with a new way of dividing the British Columbian landscape into ever smaller recognizable vegetation units, starting with four ecodomains, seven ecodivisions, 10 ecoprovinces, 30 ecoregions and 68 ecosections. This section, written by a different set of four authors, forms an anomaly: a book within a book, and what is proposed here really needs a separate review that is well beyond the scope of this one. Table 5 struck me. It provides data on the total number of bird species present in each ecoprovince and the percentage of all birds in British Columbia that nest in each ecoprovince. The three ecoprovinces showing the greatest diversity of breeding species are precisely those that are most threatened by human population pressure and large scale habitat alteration. It is unfortunate that the species accounts that follow do not refer to the vegetation section which makes it stand out as an anomaly even more. It is not clear whether this lack of integration is an oversight, the result of time constraints, or a silent admission that if a landscape unit becomes too small, it is hard to find a species that fits it. Pages 143 and 144 document the huge changes in the environment that have taken place, mostly in the last 50–100 years. These two pages might be profitable reading for those provincial politicians who have learned only recently how to spell environment.

The rest of Volume 1 and all of Volume 2 is devoted to species accounts. The species accounts provide information on the following topics: *Range* of the species within and outside of B.C., *Status* within B.C., *Nonbreeding* distribution and migration patterns, *Breeding,* including breeding habitat, nest site, materials, nest dimensions, egg dates, clutch size, incubation period, period when young are present, and nestling period. A *Remarks* section deals with a wide range of important or interesting aspects not mentioned earlier as well as references to additional literature. The data base for the species accounts includes B.C. specimen data gathered from museums throughout North America, transcribed field notes from naturalists and ornithologists, and documented observations from naturalists and birders, the published and unpublished ornithological literature, the B.C. Nest Record Scheme and the B.C. Photo-Records File—a vast undertaking. Rigorous criteria were used to accept or reject evidence of breeding. The data in the breeding section are quantified in a useful and precise manner, and when information is lacking, this is stated to stimulate further investigation.

For each species, there is a large distribution map on which circles depict the presence or absence of a species within a grid of 15 minutes latitude and 30 minutes longitude. A simple, but very effective, color-coding system within the circles shows where and when each species breeds and/or occurs. The number of sightings or nests for each month is shown at the bottom of the map. Considering where most people in British Columbia live and the remoteness of much of the province, it comes as no surprise that large areas are without circles. There is lots of room here for further study and exploration. Each species map has a small illustration by Michael Hames. These illustrations add much to the appeal of the volumes, and they help to reinforce the impression that these books were put together with great care.

Both volumes provide information on casual, accidental, extirpated, and extinct species, as well as species of hypothetical occurrence lacking adequate documentation. Three appendices provide, respectively, the dates of arrival and departure and peak movement dates of regular spring and fall migrants for various locations in British Columbia, published Christmas Bird Counts from 1957–1984, and a list of the 4626 contributors to the project. A bibliography of ca 2000 entries completes each volume.

The last summary of the bird fauna of B.C. (J. A. Munro and I. Mct. Cowan, British

Columbia Provincial Museum Special Publication No. 2, Victoria, B.C.) appeared in 1947. That important work in British Columbian ornithological history stressed taxonomy, distribution, and migration. The current volumes provide much new material on distribution and migration and quantitative information on breeding biology heretofore not available for the province and they point out the gaps in our knowledge. The challenge is there.—N. A. M. Verbeek.

The Atlas of Breeding Birds of Michigan. By Richard Brewer, Gail A. McPeek, and Raymond J. Adams, Jr. Michigan State Univ. Press, East Lansing, Michigan. 1991:xvii + 594 pp., numerous figures, maps, and tables. $39.95.—This is a handsome, scholarly book which summarizes a comprehensive survey of the breeding birds of Michigan, including 233 species (215 confirmed breeders, 12 probables and 6 possibles). Each species is treated separately in an individual description of occurrence and habitat. Each account has a black-and-white line drawing of the species and a full-page map of the breeding evidence for that bird. Individual species accounts were written by one or two authorities. As a result, several dozen people contributed to the accounts or the accompanying artwork.

Anyone glancing at this text will immediately be impressed by the attractive illustrations, readable text, and colorful and sturdy binding. Those familiar with state atlas work will be struck by the thorough coverage of the species of the state and the clarity of analysis and illustration of the breeding activities of these species. The authors should be congratulated for their achievements in incorporating and organizing the efforts of so many ornithologists.

Those who look more closely at this book will be rewarded by the rich amount of information available in it. Furthermore, typographical errors seem to be nearly absent and the style and format are consistent. The line drawings of each species also maintain remarkable consistency, given that several artists were involved. I was impressed with many of these since they often gave the impression that the artist understood the behavior of the bird being represented.

Those interested in Michigan birds absolutely must have a copy of this book. It is amazing that the price is so reasonable. Books of this quality and mass typically cost twice as much as the present volume. I encourage birders in the process of producing a state atlas to see this volume. It will rank as one of the finest of its kind.—C. R. Blem.

Utah Birds: Historical Perspectives and Bibliography. By William H. Behle. Utah Museum of Natural History, University of Utah, Salt Lake City, Utah 84112 USA. 1990: 355 pp., 139 illustrations. $25.00.—It is a great honor to offer this review of William H. Behle's latest book. This "grand man" of Utah Ornithology has produced yet another solid piece of ornithological information. This book, coupled with his earlier works, provides us with as complete a description as possible of Utah birds, bird habitats, ornithologists (both professional and amateur), collections, and suggestions for future research. In fact, this series of publications rivals that of any other single state.

This book takes a different slant than Behle's previous works. It focuses on people and events rather than on the distribution and systematics of birds. The approach is refreshing. I was captivated by the nature and tone of the book and amazed at the scholarship involved at piecing together such a complex mass of facts into a coherently wonderful story. Where did he find such detail?

Early chapters deal with three major time periods of ornithological development in the region; the pre-pioneer period (1776–1846), the colonization of the area by members of the Church of Jesus Christ of Latter-day Saints (Mormons) beginning in 1847, and the rise of

U.S. government sponsored natural history surveys during the years of 1849–1891. The now apocryphal story of the "crickets and the seagulls (sic)" is covered in detail and, I might add, put in its appropriate place.

Next, the emphasis shifts to independent collectors and university/museum-sponsored research in the Great Basin Region. In addition, these middle chapters cover the lives and contributions of all people who, even tangentially, contributed to the body of knowledge dealing with Utah birds. As the title says, this book is about Utah ornithology and contributions made by these folks to other locales largely are ignored. Nonetheless, this portion of the book is absolutely fascinating. Much of this section is made up of biographical sketches of each person who contributed to Utah ornithology. These biographies are organized in chapters or subchapters by occupation, avocation employing institution, or geographic region.

Two chapters of biological interest deal with avifaunal changes in recorded times (Chapter 16), the distinctive aspects of Utah birds, and the ornithologists who studied them (Chapter 17). Behle documents the wanton destruction, of almost anything that flew, that took place from the time the pioneers arrived until surprisingly recent times. Also documented as causing the current decline seen in many species of birds are the use of pesticides, habitat change caused by severe overgrazing and land development, and regional climatic changes (seasonal drought, etc.). Utah holds a unique place in the study of ornithology. The state possesses a wide range of very diverse ecosystems, ranging from boreal forests in the high Uintah Mountains and Deep Creek Mountains (the latter being an island completely surrounded by Great Basin Desert, to lower desert habitats such as those of the southwestern corner, Washington County or "Utah's Dixie," including the Beaver Dam Wash where, with the help of the Nature Conservancy, Brigham Young University has established a field station. The Great Salt Lake, by itself, is biologically unique but the avifauna that is attracted to it borders on amazing. Several bird species are found there that are found nowhere else in the region, e.g., White Pelican (*Pelecanus erythrorhynchos*). The Beaver Dam Wash features such southern desert species as the Wied's Crested Flycatcher (*Myiarchus tyrannulus*), Cassin's Kingbird (*Tyrannus vaciferans*), Abert's Towhee (*Pipilo aberti*), Summer Tanager (*Piranga rubra*) and Lucy's Warbler (*Vermivora luciae*), which are not commonly found in other parts of the state.

As with many locales, game birds take center stage when funds are allocated, and this is definitely true in Utah. However, research on raptors was elevated to a high level in the 1970s led by groups of professors at both Utah State Univ. and Brigham Young Univ., notably James Gessaman, Joseph Murphy, and Clayton White. This work produced numerous graduate degrees and resulted in many publications, all of which are summarized in this book.

Behle is overly modest in summarizing his own contributions to the study of birds in Utah, although most would agree that he has led the way for many of us who have studied in the state. I have noted, over the years, that he always has time to talk "birds" with anyone any time. He has been willing to provide specimens, field notes, reprints, etc. often at short notice and his enthusiasm for the study of birds in Utah is boundless. This is certainly reflected in his latest book.—Robert C. Whitmore.

Cheyenne Bottoms. Wetlands in Jeopardy. By John L. Zimmerman. University Press of Kansas, Lawrence, Kansas. 1991:197 pp., 15 color photos and 40 line drawings. $19.95.—Wetlands continue to be in jeopardy. Cheyenne Bottoms has been under seige for some time. In this book, John Zimmerman provides us a popularized account of the lengthy and rather technical work released in 1987 by the Kansas Biological and Geological surveys

entitled "Cheyenne Bottoms. An Environmental Assessment." Each of the chapters summarizes a portion of the story that intertwines into an enlightening and enjoyable description of what is known about this wetland ecosystem, its geologic and political history, the societal and cultural impacts and developments that have led to its recent troubles, an assessment of the short term solutions and last, the impact of saving Cheyenne Bottoms. Saving Cheyenne Bottoms will not only solve the critical needs of the wildlife there but it will also provide us hope for solving other environmental problems of a long-term nature. This book is well written and edited. It contains numerous personal anecdotes that bring the book to life. The color photos add to the appeal of the book and the line drawings by Martin B. Capron add a special touch in helping the reader relate to the topic. It is easy to read and understand. The book is of primary interest to those that have an interest in nature but will educate the novice as well as the expert about this fascinating habitat. Too many of our environmental problems today tend to cause frustration or apathy because of a sense of hopelessness. This book could serve as a primer on environmental problems of today, but with a twist, for it uses an example that does have hope of being solved. Cheyenne Bottoms may be given a second chance, thanks to the efforts of highly motivated people such as Jan Garton, who wrote the book's foreword. I recommend this book to community, high school and college libraries and to readers who are looking for an educational and entertaining book.—Roger L. Boyd.

A Naturalist in New Guinea. By Bruce M. Beehler, illus. by John Anderton. Univ. of Texas Press, Austin, Texas. 1991:251 pp., 26 color photos, 30 line drawings, 7 maps. $26.95 cloth.—This book chronicles more than a decade of ornithological research by the author, mostly on the ecology of birds-of-paradise. In the introduction, Beehler describes the plan and purpose of the book, which he decided to write after watching his wife's reactions to the novelty of New Guinea on her first visit. The purpose of the book is to ". . . serve as a lay introduction to the island's natural history and a sort of catalog of the things naturalists do when out in the forest." This purpose has been admirably achieved. Although most of Beehler's research is on birds, he is clearly a broadly based naturalist/ecologist, and the book presents a balanced ecological perspective, with botany receiving a major focus, and with amphibians, insects, and mammals skillfully woven into the ecological fabric. The author's digressions into the cultural aspects of the Papuan natives add flavor and interest.

This is a very personal narrative describing, essentially chronologically, the author's many trips to wild places in New Guinea. He describes his research on birds-of-paradise in layman's terms, and, although much of his work has been published in journals, the often harsh conditions and unpredictable circumstances under which much of the research was conducted provides some new insight into the challenges faced by researchers working under primitive conditions in remote tropical forests.

The book is organized into an introduction and nine chapters, with maps that provide a useful visual context for the narrative. The first three chapters concern Beehler's first impressions as he learns about his new environment at and around the Wau Institute of Ecology. We read of the capital city, Port Moresby, with the betel nut (mildly narcotic) chewing natives, his initial experiences with setting up camps in the rainforest, muddy conditions, and cutting trails through "a wall of raspberry vines and bamboo," which was ". . . like trying to cut through barbed wire with a bread knife." The descriptive text is interspersed with digressions into the possible evolution of mimicry of the Helmeted Friarbird (*Philemon buceroides*) by the Brown Oriole (*Oriolus szalayi*) and a general discussion of bowerbirds and bowers. A trip to the Huon Peninsula involved collecting birds for the National Museum of Natural History of the Smithsonian Institution, and Beehler offers a rather eloquent

defense of bird-collecting for museums. A substantial account of New Guinea during World War II adds an interesting historical and cultural perspective.

Succeeding chapters deal with expeditions to Goodenough Island, Beehler's doctoral dissertation work near Wau, the highlands of western Papua, Irian Jaya (western New Guinea), the lowland forests, and the tropical mountain tundra. On Goodenough Island the author searched unsuccessfully for a reported "black bird," which might have been an undescribed bird-of-paradise, but concludes that getting out into the field for ". . . sights of little-known birds in rarely visited forests" was worth the effort and hardship.

His dissertation work focused on the evolution of bird-of-paradise reproductive behavior through an interspecific comparison of a monogamous manucode and three polygamous species. There is much of interest for the ornithologist as well as the target lay audience. Of particular note are the complex bird and food-plant relationships. For example, the manucode specializes in figs of low nutritional value, and Beehler concludes, "It seems safe to say that the manucodes are monogamous because both parents are required at the nest to provision the offspring." His highland work concerned bird-of-paradise species not found in his dissertation study sites. Tales of astrapias and sicklebills are interspersed with descriptions of the highland natives and their fantastic ceremonial dress for *sing sing* tribal gatherings, the purchase of wives, and the still prevalent tribal warfare. Lowland expeditions in the ". . . claustrophobic, breathless humidity of the jungle interior," one of which was on his honeymoon, featured contrasting tales of leeches, biting insects, tropical ulcers, and torrential rains on one hand, and of Palm Cockatoos (*Probosciger aterrimus*), crowned pigeons, and cassowarys on the other. Scientific aspects focused on the little-known Pale-billed Sicklebill (*Epimachus bruijnii*).

The final chapter tells of the long and difficult trek to the alpine tundra where the author hoped to unravel some of the mysteries surrounding the Macgregor's Bird-of-Paradise (*Macgregoria pulchra*). He reports some of his previously unpublished results concerning the ephemeral nature of this species's major food resource, *Dacrycarpus* fruit, and the resulting disappearance of the birds from his study site. Some tropical environments, apparently, are neither predictable nor benign. It is perhaps in his descriptions of camping for the first night in these surroundings, huddled beside a campfire watching the stars, that best exemplifies his passion for the wilds of New Guinea, "My memory of that first night at Lake Omha burns through the mist of passing years. It is for memories of nights like that, in places like that, that I keep returning to New Guinea."

Beehler concludes with a discussion of the complexities of New Guinea forest ecology and the corresponding difficulties that conservationists face in long-term planning. He suggests that the international community must foster educational opportunities for native New Guinea naturalists and concludes, "It is now time to share the excitement and responsibilities of studying these tropical forests with those who will ultimately have to decide their fate."

I found little to fault in this book. It is attractive and apparently error-free. The line drawings are excellent and nicely compliment the color photographs by the author. The only thing that bothered me was the type face which reduced punctuation marks to near invisibility. I was also surprised by the inclusion in the text of scientific names for plants and all animals except for birds, a sacrifice to readability I presume. The scientific names of birds are, however, included in the index so they can be looked up.

This book paints a vivid picture of wild conditions on a major ornithological frontier. The science is presented clearly and with much insight. It should prove very informative for the lay audience for which it is intended, and there are lots of nuggets for the ornithologist to mine as well. I recommend this book to anyone who plans to travel or work in New Guinea, or enjoys informative vicarious adventures in natural history.—WILLIAM E. DAVIS, JR.

THE FRAGILE SOUTH PACIFIC: AN ECOLOGICAL ODYSSEY. By Andrew Mitchell. Univ. of Texas Press, Austin, Texas. 1991:280 pp., 39 color photos, 7 maps. $24.95 cloth.—This book describes the personal odyssey of the author who followed from west to east through the major islands of the South Pacific the probable historical dispersal path of plants and animals, including man. At each stepping-stone along the way, he asks the questions: "How did plants and animals reach this archipelago? How has evolution shaped the present day flora and fauna? What happened when man arrived? What is the state of the environment today?"

The narrative is a broadly based natural history and cultural exploration which is well written, very readable, and spiced with imagery and descriptive metaphors—describing volcanic islands as ". . . remnants of ancient high volcanoes which poke their heads above the blue surface like fluted emeralds," ". . . Simbo lay on the horizon like a crouching turtle, a grey outline against the stormy Solomon sky," or ". . . the sky darkens to a bruise." The book is a charming description of modern travel and ecological adventure. The author presents the geological setting with a discussion of plate tectonics, coral reefs, and deep water trenches. The seven maps provide a helpful visual framework for the text.

The book is organized into 10 chapters which are mostly narratives of visits by the author to island groups including the Carolinas, Solomons, Fiji, Tonga, Samoa, Hawaiian, Society, and ending with Easter Island, interwoven with commentary on the geology, natural history, and cultural history of man. The chronicle of human adventure includes the discovery of each island group by western man, and traces the exploitation and effects, mostly negative, which followed. There are stories of head hunters, cannibals, the discoveries and violent death of Captain Cook, discussion of the three major groups of peoples who are indigenous to the islands (Micronesians, Melanesians, and Polynesians), and the origin and evolution of the various languages. There is an ample smattering of archeology and anthropology, early theories of lost continents, and arguments over the ancestry of the occupants of Easter Island.

The ecological discussions are broadly based taxonomically, ranging from botany to coral reefs, iguanas, skinks, fruit bats, and, of course, birds. Birds, however, are not the major focus of this work. Seven of the 39 color photographs are bird related, and this is a good index of the ornithological content of the book. The treatment of ornithological matters is somewhat uneven. For example, the author describes megapode farming but does not give the common or latin name of the megapode species, but does provide both names in his discussion of pygmy-parrots. He provides general natural history commentary on many of the more exotic birds such as hornbills and echolocating swiftlets. He describes the adaptive radiation of the Hawaiian honeycreepers, the demise of Hawaii's endemic bird species, the influence of avian malaria, the conservation story of the Nene or Hawaiian Goose (*Nesochen sandvicensis*). He talks of moas, the feather trade, and a host of conservation issues involving birds. In a book of such broad ecological scope the treatment of birds is necessarily superficial, and statements such as ". . . the lek is not an open piece of grassland, as for the cock-of-the-rock . . . ," or "Petrels tend only to fly at night . . ." do not inspire great confidence in some of the ornithological pronouncements. The author also does not adequately discuss the recent avian paleontologic work which suggests that the effect of man on island avian communities is even greater than had been previously recognized.

The author presents a conservation message, often in a somewhat polemical tone, but the large number of endemic species, burgeoning human population, and difficult political situations make this tone appropriate. He presents case histories, such as the Levers Pacific Timbers deal in the Solomon Islands, in an even handed manner and points out the complexities involved in conservation issues. He discusses the ecological disasters resulting from nuclear testing, the geopolitics of U.S. military strategy and island bases, and the tenacious

colonialism of the French. One cannot escape the realization that the islands of the South Pacific need more attention from the conservation organizations of the world. Excluding Hawaii, there are only 50 islands which have protected areas, and the author's guide to national parks and protected areas is only six pages long.

The bibliography contains 71 references which include a few journal articles and reports, but unfortunately there is no referencing in the text, a sacrifice to readability no doubt, so that the value of the bibliography is severely diminished. Although the book has only limited ornithological value, I would recommend it to anyone who plans to travel to the South Pacific. Its broad cultural and ecological scope provides a wealth of information which should be of interest to any visitor to the area.—William E. Davis, Jr.

Life of the Pigeon. By Alexander F. Skutch, illus. by Dana Gardner. Cornell Univ. Press, Ithaca, New York. 1991:130 pp., 24 color plates with caption figs., 29 text figures, 4 tables. $49.95.—Alexander Skutch has few peers as an observer of the life of birds. With more than 20 books to his credit, he also has few peers as a prolific communicator of his observations. In "Life of the Pigeon," as in his previous books, "Life of the Tanager," and "Life of the Woodpecker," Skutch teams up with artist Dana Gardner to produce a book that is both readable and educational.

Skutch combines his personal knowledge of pigeons that he has watched near his Costa Rican home with a masterful summary of the published literature on columbids of the world. After a brief introduction to the family Columbidae with its nearly 300 species, Skutch provides a chapter-by-chapter accounting of the main elements of their behavioral ecology. Consistent with Skutch's interests, reproductive aspects—from courtship to the rate of reproduction—take up the bulk of the book. The final brief chapters discuss pigeon-human relations, homing pigeons, navigation, and a fascinating description of the various races of pigeons kept by Charles Darwin. A bibliography and an index follow the text.

Skutch's writing style is unusual, to say the least. Each chapter is a nonstop narrative, unimpeded by headings or breaks of any sort. Within each chapter, there is little discernable pattern to the arrangement of topics and facts about the various species that illustrate those topics. Anecdotes are thrown in along with data, mixing trivia with important information. Although acknowledgements are given to authors of major studies, no distinction is made between Skutch's personal observations and those of other naturalists. For example, in a discussion of foraging behavior, Skutch notes that Galapagos Doves (*Zenaida galapagoensis*) dig with their bills. Then it is stated, "A Galapagos Dove continued for many minutes to dig beneath an opuntia bush . . ." (p. 13). It is unclear whether Skutch had seen this himself or is reporting on something he read. It is also unclear why this observation even merits repeating.

Despite these difficulties in presenting scientific information in a popular style, the book is very readable. The text flows well. At the end of each chapter, the reader will have a feel for how doves and pigeons eat and drink, nest, navigate or whatever the topic may be.

I found no errors in the text, although poorly substantiated information such as the assertion of life-long pairbonds among permanently resident Mourning Doves (*Zenaida macroura*) is presented as fact (p. 22). Also, the illustration of the Tooth-billed Pigeon (*Didunculus strigirostris*) perpetuates the fallacy that this species is a ground-dweller. Skutch's well-known species-selectionist views and slight anthropomorphism surface at times, but can easily be ignored without detracting from the information content.

The two dozen plates by Dana Gardner dispel any notion that pigeons are drab, dull birds. A sampling of the showier pigeons around the world emphasizes the diversity of plumages and sizes within the basic body format. Gardner's images are vivid, but many of the shapes

look like cardboard cut-outs against a bare background. The beautiful painting of a pair of Victoria Crowned Pigeons (*Goura victoria*) in their natural habitat, which graces the book jacket, is an exception but still does not illustrate the behavior of the birds.

The doves and pigeons of the world are a fascinating lot. Alexander Skutch, aided by Dana Gardner, captures the essence of their life and presents it in an easily digestible form. Although scientists may be exasperated by some of the elements of the presentation, any student of birds will be enlightened and entertained by reading "Life of the Pigeon."—David E. Blockstein.

Hunters of the African Sky. Text by Peter Steyn, color plates by Graeme Arnott. Struik Winchester (P.O. Box 3755, Cape Town 8000 South Africa). 1990:96 pp., frontispiece (soaring Bateleurs!), 34 numbered, 9 unnumbered color plates (10 × 14½) by Graeme Arnott. (Dust jacket with Bateleurs and Bearded Vulture.) ISBN Q 947439 17 2. Standard edition, cloth, R 135. $48.00—This handsome volume is a raptorphile's delight. Featuring enlarged versions of the original 24 plates illustrating the "Birds of Prey of Southern Africa" by Steyn (1982), it includes another 10 plates of 'illustration' and also a number of 'Artist's plates' showing anatomical features and feather detail necessary for completion of definitive plates.

The larger format does for Arnott's paintings much of what the publication of the plates for Robert's "Birds of South Africa" some years back did for the paintings of Norman Lighton.

In the present 1990 volume, American viewers not only have an arresting fresh view of Africa's unmatched raptor assemblage but also an opportunity to appraise and admire the artistry of Graeme Arnott, a relative newcomer in the front rank of wildlife artists. A native of Zimbabwe, he has worked closely with Peter Steyn for many years and recently contributed a number of plates to Valerie Gargett's "The Black Eagle" (1990).

I find the plates so fascinating that I wish I had each of them separately framed . . . even the repeated figures of the 'overhead' views appear freshly anew each time I look at them. . . . plate 15 with 18 figures of eight species of vultures and two of the Secretary Bird, each vividly distinct, painted against a pale blue sky; plate 18 with 16 figures of 10 species of some perhaps lesser known eagles; plate 20 with 17 figures of nine species: Crowned Eagle (*Stephanoaetus coronatus*), Martial Eagle (*Polemaetus bellicosus*), Bateleur (*Terathopius ecaudatus*), Verreaux's Eagle (*Aquila verreauxii*), hawk-eagles (Sp.?), and Long-crested Eagle (*Lophaetus occipitalis*); . . . these plates simply have to be seen as I can't find words for them.

The text by Peter Steyn is well-suited to the plates and contains much up-to-the-present information, but the real impact of this splendid volume is in the aesthetic . . . even the 'dust-jacket'!—Walter R. Spofford.

Computer Intensive Methods for Testing Hypotheses. By Eric W. Noreen. John Wiley, New York. 1989. $39.95.—This book will be helpful and thought-provoking for anyone who analyzes data. The three chapters that make up the body of the text provide an accessible introduction to three powerful statistical tools: randomization, Monte Carlo simulations, and bootstrapping. Noreen's last chapter summarizes all three methods, compares them to each other and to their corresponding parametric equivalents, and suggests when each might best be used. These are easily used alternatives to traditional parametric tests and are appropriate whenever an experimenter (or critical reviewer) isn't certain that parametric assumptions are appropriate. Although these methods are not new to ornithology, e.g., Schoener (pp. 254–281 in Strong et al. [eds.]. Ecological communities: conceptual issues and

the evidence, Princeton, 1984) uses randomization tests in examining *Accipiter* communities and Lanyon (Auk 104:144–146, 1987) describes the use of bootstrapped Monte Carlo sampling in ornithological studies, Noreen's discussion of these tests will make them more accessible to many ornithologists. Noreen takes an economic perspective in his examples, but they are readily transferable to many ornithological problems. This review briefly describes these methods, their advantages over traditional parametric tests, and some of their limitations.

Computer-intensive methods are statistical methods which use substantially more computer resources than traditional parametric tests (hence their name), but which can be used easily on personal computers. Parametric tests were developed when it was prohibitively expensive to conduct the precomputer-era equivalent of computer-intensive statistics. Parametric assumptions (e.g., that errors have mathematically "nice" distributions) permit researchers to calculate the *ex ante* probability of certain associations relatively simply. However, the tradeoff for this simplicity is that the underlying assumptions are also implicitly being tested with every hypothesis test. For example, a least squares univariate regression is a *joint* test of the underlying parametric assumptions and the hypothesis that the independent variable's coefficient is zero; if the null hypothesis is rejected, it means either that the underlying assumptions are violated and/or that the independent variable's coefficient is nonzero. Consequently, a "statistically significant" rejection of a null hypothesis is often accompanied by a nagging uncertainty about whether the results reflect a nonrandom association or merely inappropriate parametric assumptions. Computer-intensive statistics let researchers avoid the standard parametric assumptions often without having to give up the power of parametric tests.

Randomization (Chapter 2) is used to test hypotheses about relationships between variables, and can be a substitute for a *t*-test of differences between means, *t*-tests on coefficients in parametric regression, analysis of variance, etc. A typical null hypothesis for a randomization test is that one dependent variable is independent of other variables. For example, a positive correlation is observed to exist between two variables in a sample; the null hypothesis is that this observed correlation is due to chance. Randomization tests are conducted by "shuffling" (on a computer) the observed dependent variable many times with respect to the observed independent variable. The correlation is measured in each random sample. The null hypothesis is rejected only if a significantly small percentage (e.g., $<5\%$) of the random samples have correlations greater than the absolute value of the originally observed correlation (for a two-tailed test). Because randomization tests offer the power of many parametric tests without the parametric assumptions, many researchers will find them to be useful additions to their repertoire of statistical tests.

Monte Carlo sampling (Chapter 3) tests hypotheses concerning the population from which a random sample is drawn. A typical null hypothesis is that the data are a random sample from a population with a parameter which has a specified value (e.g., mean = 50 cm). Monte Carlo simulations are done by (1) drawing random samples from the theoretically specified (i.e., null hypothesis) population, (2) computing the test statistic (e.g., mean) for each random sample, (3) comparing the simulated test-statistics to the test statistic from the original data, and (4) accepting the null hypothesis if larger-than-original values of the test statistic occur in a substantial proportion (e.g., $>5\%$) of the total samples (and rejecting otherwise). Monte Carlo sampling with bootstrap resampling (see below) is especially appropriate for estimating the dispersion of statistics whose distribution is unknown, e.g., factor loadings from principal components analysis (Lanyon 1987).

Bootstrap resampling (Chapter 4) is one method for creating the null-hypothesis population from which samples are drawn in Monte Carlo simulations. (Some authors also use "boot-

strap" or "bootstrap method" to refer to Monte Carlo sampling with bootstrap resampling.) Bootstrap resampling is random sampling with replacement from the sample population.

Computer-intensive methods have limitations as well as great promise. One limitation is that these methods presently require a modest amount of programming; however, Noreen includes many examples (in Basic, Fortran, and Pascal) of programs for each method. Another important limitation is, because these methods are based on random sampling from a set of observations, hypothesis tests with computer-intensive methods are actually joint tests of the random sampling and the null hypothesis. Yet, on a computer, the "random" sample is created by a known algorithm that will always produce a predictable sequence of values (from a given starting point). One is forced to use "pseudorandom" samples (i.e., samples that are hard to distinguish from random samples if you don't know the algorithm) and, consequently, one must handle the randomizing part of computer-intensive statistics carefully. Poor "random-number" generating programs are not uncommon, and users should be cautious about using untested programs to create their pseudorandom sampling. This important point should be given greater prominence in future editions of Noreen's text. As Noreen mentions, Press et al.'s (1986, Cambridge) "Numerical Recipes" is an excellent source of simple, yet powerful, programs for creating pseudorandom numbers.—Christopher H. Stinson.

ALSO RECEIVED

The Conservation of Lowland Dry Grassland Birds in Europe. Proceedings of an international seminar held at the University of Reading 20–22 March 1991. Paul D. Goriup, Leo A. Batten, and John A. Norton (eds.). Joint Nature Conservation Committee, Peterborough, England. 1991:136 pp., many black-and-white photos and graphs. No price given.

Birds and Pastoral Agriculture in Europe. Proceedings of the Second European Forum on Birds and Pastoralism. Port Erin, Isle of Man, 26–30 Oct. 1990. D. J. Curtis, E. M. Bagna, and M. A. Curtis (eds.). Scottish Chough Study Group, Peterborough, England. 1991:137 pp., many black-and-white photos and figures. £12.50.

Waders Breeding on Wet Grasslands. Wader Study Group Bulletin, No. 61 Supplement. Hermann Hötker, (ed.). Joint Nature Conservation Committee, Peterborough, England. 1991:107 pp., many black-and-white photos and figures. No price given.

These three symposia volumes are available from the Publications Branch, Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough, PE1 1JY, England.

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Editor Charles R. Blem
Department of Biology
Virginia Commonwealth University
816 Park Avenue
Richmond, Virginia 23284-2012

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See Wilson Bulletin, 103:163–164, 1991 for more detailed "Information for Authors."

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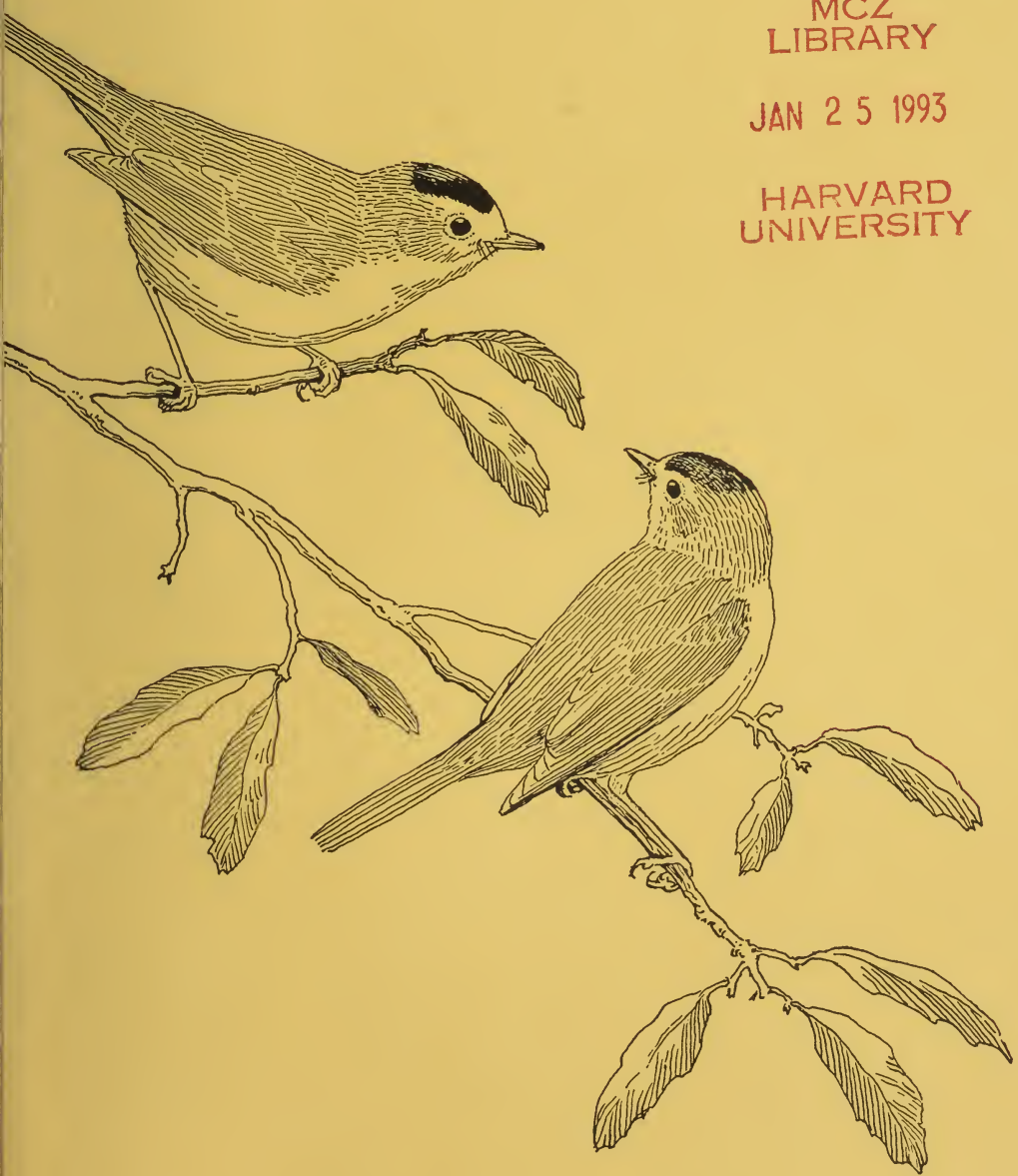

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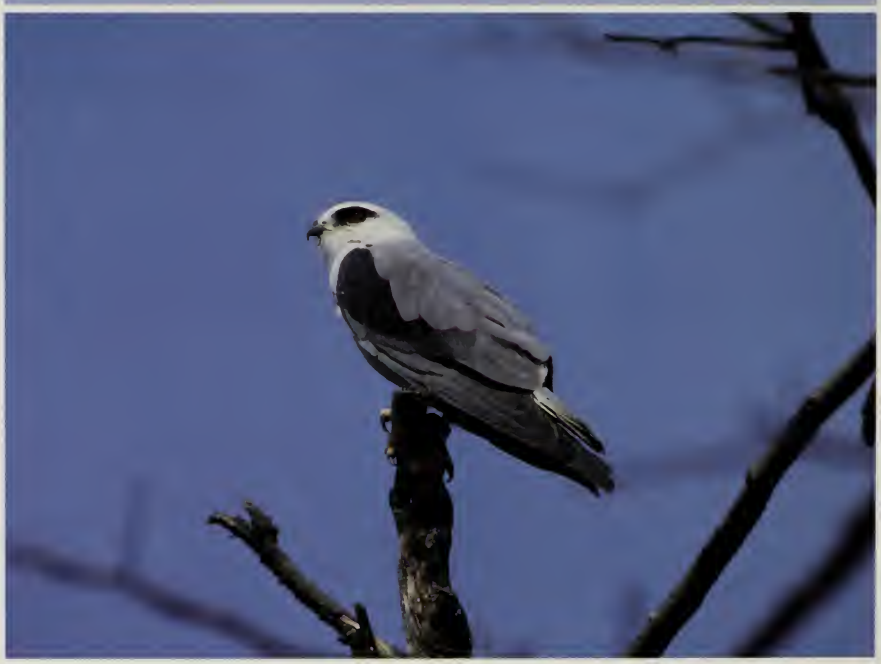

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THE TAXONOMIC STATUS OF THE WHITE-TAILED KITE

WILLIAM S. CLARK[1] AND RICHARD C. BANKS[2]

ABSTRACT.—The White-tailed Kite (*Elanus leucurus*) of the Americas has been merged with the Black-shouldered (or Black-winged) Kite (*E. caeruleus*) of the Old World and the Australian Black-shouldered Kite (*E. axillaris*) by North American authorities (but not elsewhere), primarily because of similarity in plumage. However, American kites differ from Old World kites in greater size and weight, in proportions (relatively longer tail and smaller bill and feet), plumage pattern (particularly of juveniles), and in behavior. Here we argue that these characters are sufficiently distinctive to warrant recognition of *E. leucurus* at the species level. *Received 19 May 1992, accepted 1 Sept. 1992.*

The White-tailed Kite (*Elanus leucurus*) of the Americas was long considered a species distinct from the Black-shouldered (or Black-winged) Kite (*E. caeruleus*) of the Old World, and the Australian Black-shouldered Kite (*E. axillaris*). We follow Schodde and Mason (1980) and McAllan and Bruce (1989) in the use of *axillaris* rather than *notatus* as the name for the Australian species. However, Parkes (1958) and Husain (1959) suggested that both *leucurus* and *axillaris* should be considered conspecific with *caeruleus,* and that the complex forms a superspecies with the Letter-winged Kite, *E. scriptus,* of Australia. Arguments for this merger were based primarily on the similarity of plumage. Parkes (1958) stated that, for any plumage character, forms of the combined species *E. caeruleus* could be arranged in a progressively intergrading series. Husain (1959) postulated a biogeographical scheme to account for the distribution of the forms, considering only the amount of black on the underwing.

The American Ornithologists' Union (AOU 1983), Palmer (1988), and American field guides based on AOU (1983) follow Parkes (1958) and Husain (1959) and treat the American forms under the combined name

[1] 4554 Shetland Green Rd., Alexandria, Virginia 22312.
[2] U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.

caeruleus. On the other hand, all authorities outside of and many from North America have continued to recognize *E. leucurus* and *E. axillaris* as species distinct from, but closely related to, *E. caeruleus* (Vaurie 1965, Brown and Amadon 1968, Mayr and Short 1970, Glutz von Blotzheim 1971, Condon 1975, Stresemann and Amadon 1979, Cramp and Simmons 1980, Brown et al. 1982, Amadon and Bull 1988, Short et al. 1990, and Sibley and Monroe 1990). The three taxa are often treated as allospecies.

Here we discuss differences in size, proportions, plumage, and behavior that lead us to the conclusion that *Elanus leucurus* of the Americas should be treated as a species distinct from *caeruleus* and its races. We believe that *axillaris* should similarly be considered distinct, although our study was directed less toward that form and we have no experience with it in the field. Mees (1982) suggested that several other recognized subspecies of *caeruleus* should be combined with *E. c. hypoleucus* and recognized at the same level as *caeruleus, leucurus,* and *axillaris*.

METHODS

The senior author has observed both *E. leucurus* and *E. caeruleus* in the field for many hours, *leucurus* in California, Texas, Mexico, Guatemala, and Panama, and *caeruleus* in Senegal, Kenya, Spain, and India. His notes on behavior and appearance are supplemented by information in the literature.

Plumage characters were examined on and measurements of wing chord, tail length, culmen from cere, and hallux length were taken from specimens in the American Museum of Natural History, the British Museum (Natural History), and the U.S. National Museum of Natural History. Additional sets of measurement data were obtained from the literature, as was information on weight.

RESULTS

White-tailed Kites (*E. leucurus*) differ from Black-shouldered Kites (*E. caeruleus*) in size and especially in proportions, in characteristics of the plumage, especially in young birds, and in hunting behavior and flight. Australian Black-shouldered Kites (*E. axillaris*) are similar to *caeruleus* in proportions but resemble one or the other of the Old and New World forms in plumage characters and behavior.

Size and proportions.—White-tailed Kites are considerably larger than Black-shouldered Kites (Table 1; Fig. 1), particularly in length of wing and tail. In all forms of the genus other than *E. scriptus* the sexes are similar in size and samples have been combined by many authors; females of *scriptus* are larger than males (Table 1; Brown and Amadon 1968). We attribute differences in means in samples of *leucurus* to differences in method of measurement, as several of the samples may have included the same individual specimens (Palmer 1988:135). As noted by Bangs

Table 1

Measurements (mm) from Populations in the Genus *Elanus*

Wing			Tail			Culmen			
N sex[a]	Range	$\bar{x}$	N	Range	$\bar{x}$	N	Range	$\bar{x}$	Source[b]
E. l. majusculus, North America									
10	300–324	309	10	170–181	177	9	18.0–19.1	18.7	1
25	300–325	316	25	170–188	179	25	16.5–21.0	19.2	2
14	302–328	314	14	174–186	181	14	18–19	18.7	3
20 m		316				19		19.1	4
15 f		318				15		19.5	4
9 m		309	9		184	9		18.5	5
7 f		307	7		183	7		19.2	5
E. l. leucurus, South America									
10	288–304	295	10	157–169	162	10	16.6–17.9	17.4	1
14	290–310	301	14	149–177	162	14	16.5–19.5	17.7	2
E. c. caeruleus, Europe and Africa									
13 m	249–292	271	18	108–136	118	17	15.8–17.9	17.1	6
13 f	262–297	273	13	108–127	118	15	15.9–18.2	17.2	6
E. c. caeruleus, Africa									
7	248–272	260	7	116–127	120	7	15.2–17.0	16.2	1
E. c. vociferus, Southern Asia									
9	248–278	264	9	113–130	123	9	15.2–17.9	16.7	1
E. c. sumatranus, Sumatra									
11 m	290–303	294	12	132–146	137	12	17.8–19.0		7
13 f	285–305	294	13	130–146	138	13	18.5–20.3		7
E. c. hypoleucus, Java									
16 m	292–310	298	18	132–150	140	18	18.8–19.8		7
16 f	294–310	302	18	131–151	142	18	19.0–20.8		7
E. c. wahgiensis, New Guinea									
—		297							8
E. axillaris, Australia									
6	291–298	294	6	136–142	139				1
— m	280–302	294	—	142–153					8
— f	280–310	298	—	142–154					8
E. scriptus, Australia									
— m	292–296		—	146–150					8
— f	302–313		—	156–162					8

[a] Sexes combined unless indicated (m for male, f for female).

[b] Sources: 1, this study; 2, Bangs and Pennard (1920); 3, Friedmann (1950); 4, Snyder and Wiley (1976); 5, Havbecker (1942); 6, Cramp and Simmons (1980); 7, Mees (1982); 8, Brown and Amadon (1968).

FIG. 1. Two specimens of *E. caeruleus* (left) and two of *E. leucurus* (right) showing dorsal (above) and ventral (below) surfaces. Note differences in size, relative lengths of tails, and back color.

TABLE 2

WING/TAIL RATIOS OF SEVERAL POPULATIONS OF *ELANUS* (BASED ON DATA IN TABLE 1)

Species	Population	Range of ratio
Elanus leucurus	North America	1.70–1.80
E. leucurus	South America	1.75–1.86
E. caeruleus	Africa	2.05–2.28
E. caeruleus	Asia	2.05–2.28
E. "hypoleucus"	Sumatra, Java	2.14[a]
E. axillaris	Australia	2.06–2.14
E. scriptus	Australia	1.93–1.99

[a] From data in Mees (1982).

and Pennard (1920), North American White-tailed Kites, *E. l. majusculus,* are somewhat larger than South American birds, *E. l. leucurus.* The latter are nevertheless notably larger than Old World *caeruleus* and Australian *axillaris.* The populations constituting *hypoleucus* of Mees (1982) are close to the size of American birds in wing chord measurements but have much shorter tails (Table 1).

The difference in tail length between *leucurus* and *caeruleus* is greater than the difference in wing length (Table 1). This difference in proportions may be best appreciated from calculation of the wing/tail ratio. In all American birds, this ratio is less than 2.0; in Old World birds and in those of Australia it is invariably more than 2.0 (Table 2). The ratio is intermediate in *E. scriptus.* This proportional difference is particularly noticeable on perched birds of both forms. On perched *leucurus* the wing tips do not extend to the tail tip, whereas on perched *caeruleus* they project far beyond the tail tip (Frontispiece).

Lengths of the culmen (Table 1) and hallux (data not shown; sample means 15.7–16.5 mm) are similar throughout the complex and cannot be used to separate *leucurus* and *caeruleus.* However, as *caeruleus* is smaller, the bill and feet are proportionally larger; in particular, *caeruleus* appears larger headed than does *leucurus* (Frontispiece).

Mendelsohn and Jaksic (1989) summarized weight data, and showed that American *leucurus* averages 50–65 g heavier than African *caeruleus*; Australian *axillaris* is intermediate, but is nearer to South American *leucurus.*

Data summarized by Mendelsohn and Jaksic (1989) indicate that the length of the secondaries in Californian *E. l. majusculus* and African *E. caeruleus* is similar (158 vs 146 mm, respectively), but as *leucurus* is larger

and longer winged, the wing shapes of the two are different. This and the differences in relative tail length result in quite different shapes of flying White-tailed Kites and Black-shouldered Kites. According to Mendelsohn and Jaksic (1989), *leucurus* has both a higher aspect ratio and a much greater wing area than does *caeruleus* (1001 vs 843 cm^2).

Plumage.—*E. leucurus* and *E. axillaris* have a patch of black underwing coverts at the base of the primaries. This patch is lacking in *E. caeruleus,* although some individuals of that species have a few coverts with dusky tips (Husain 1959). The lower surface of the primaries is dark in *leucurus, axillaris,* and most *caeruleus.* The primaries are nearly white below, with a variable amount of gray on the wing tip, in *E. c. hypoleucus* and *E. c. sumatranus* (Salomonsen 1953), and apparently in *E. c. wahgiensis* (Mayr and Gilliard 1954).

The outer five pairs of rectrices of young *leucurus* are white, with a variable amount of pale gray on the distal portion of the outer webs. On all but the outer pair the gray extends onto the inner web forming a continuous subterminal tail band. The central rectrices are entirely gray except for a narrow white tip. The gray on the rectrices is darker and seldom, if ever, forms a band across the tip of the tail in young *caeruleus,* usually being restricted to the outer webs. In *E. c. hypoleucus* and in *E. axillaris,* the gray on the tail is much reduced and except for the central rectrices the tail is essentially white.

Behavior.—White-tailed Kites hunt almost exclusively by hovering; Jaksic et al. (1987) reported seeing only four instances of hunting from perches during observations of 80 hover-hunts in Chile. Australian *axillaris,* like *leucurus,* hunts mostly by hovering (R. Schodde, pers. comm.). After reviewing the literature, Mendelsohn and Jaksic (1989) could report no observations of perch-hunting from North America. On the other hand, Old World Black-shouldered Kites hunt regularly from perches (Mendelsohn and Jaksic 1989), hunting from the hover only about 30% of the time (Tarboton 1978), although the proportional number of hunting events (as opposed to time spent) is not given. Clark and P. Bloom were able to capture perched Black-shouldered Kites in India easily using bal-chatri traps with mice. Bloom (pers. comm.) was able to capture only one White-tailed Kite in California using the same trap with mice out of more than 200 attempts. The one caught was undernourished and was captured outside of the breeding range of the kite.

Differences in hunting methods may be related to differences in prey selection. The White-tail is a rodent specialist, whereas the Black-shoulder, at least in some areas, takes a wider selection of prey including birds and lizards (Cramp and Simmons 1980, Palmer 1988:147). White-tails catch prey twice as quickly as do Black-shoulders from hovers (Mendelsohn and Jaksic 1989).

Black-shoulders often cock the tail up over their backs and then down (tail-bobbing of Palmer 1988:145); Tarboton (1978) reported tail-cocking during 14% of perch-hunting time, when intensely excited just before or after a strike. Although Steyn (1963) had previously linked tail-cocking to excitement, Mendelsohn and Jaksic (1989) suggested that it served to warn other birds away from the hunting area. Goriup (1981) reported tail-cocking during preening in Portugal. This behavior is seldom reported for White-tails (Brooks 1943). Despite many hours of observation, WSC has observed only one instance of tail-bobbing in American kites, by an adult female in California being harassed by her begging young.

Black-shouldered Kites often perch with their folded wings drooped below the tail whereas White-tailed Kites usually perch with the wing tips folded over the tail (Frontispiece), but both can hold their wings either way. A perched Australian Black-shouldered Kite is illustrated with the wings folded over the tail (Macdonald 1973), the usual posture for that species (R. Schodde, pers. comm.).

White-tailed Kites are somewhat communal and nest in fairly close proximity to one another and defend territories weakly. Watson (1940) reported some fighting by White-tails in the establishment of territories but noted that pairs often breed communally when prey are abundant. Peyton (1915) found two nests within 200 yards (184 m), and Pickwell (1930) reported three nests at points of a triangle measuring 320, 200, and 175 yards (294, 184, and 161 m). Hawbecker (1942:269) reported two pairs nesting within 400 yards (368 m) of one another, with only one aggressive encounter. Dixon et al. (1957) reported three nests within a radius of 500 feet (153 m), with two others in adjoining groves, and saw no territorial fighting. On the other hand, Black-shouldered Kites are strong in their territorial defense; Mendelsohn (1983) reported that South African birds defended their territories vigorously and persistently, where average territory size ranged from about 2.4 to about 4.5 km^2. However, Madden (1977) found two nests in South Africa that were approximately 200 m apart.

DISCUSSION

The inclusion of *leucurus* with *caeruleus* by the AOU was based mainly on Parkes (1958), and to a lesser extent on Husain (1959). Parkes (1958) made two points to support this merger. First, that one could arrange specimens of both forms progressively in an intergrading series and second, that these forms resemble each other more than do subspecies of some other raptors, specifically *Accipiter gentilis, A. striatus,* and *Falco peregrinus.*

We have found that *E. leucurus* can always be separated from *E. caeruleus* by the presence of black carpal patches and by a wing/tail ratio less

than 2.0; *caeruleus* lacks the black carpal patch and has a wing/tail ratio greater than 2.0.

Clark has observed in the field on different continents two or more races of 12 species of diurnal raptors, including *Accipiter gentilis* and *Falco peregrinus*. Although plumage can vary greatly between races of some of these species, none show the differences in behavior and overall proportions exhibited between *leucurus* and *caeruleus* as presented above.

We believe that the characters of the American birds are sufficiently distinctive to warrant recognition of the White-tailed Kite *E. leucurus* at the species level.

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COLOR PLATE

The frontispiece photographs by W. S. Clark and B. K. Wheeler have been made possible by an endowment established by George Miksch Sutton.

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MIGRATION OF WOODLAND BIRDS AT A FRAGMENTED INLAND STOPOVER SITE

KEVIN WINKER,[1] DWAIN W. WARNER,[1] AND A. R. WEISBROD[1,2]

ABSTRACT.—The abundance, timing, and habitat distribution of woodland-associated migrants were examined at a migratory stopover site in the St. Croix River Valley, Washington County, Minnesota during spring and autumn migrations, 1984–1986. Five wooded habitats (1–3+ ha) were studied using mist nets. Migrants made up 92% of the species (N = 100) and 94.8% of the individuals (N = 17,019) captured. Of the 69 most common migrant species, 58 (84%) were Nearctic-Neotropic migrants. Analyses of median passage dates suggest that peak numbers, and thus resource demands, occurred in the days surrounding 14 May and 31 August. Eighteen migrant species (53% of those adequately covered by our study periods) showed a difference between median spring and autumn passage of 105 days or less, and thus spend less than 30% of their annual life cycles on their breeding grounds. Seasonal absences or higher capture rates in spring suggest that seven species in our region use migratory routes differing from the regional norm. The distributions of birds at our site changed between seasons, suggesting a spatial shift in habitat use by the entire avian community. *Received 9 Dec. 1991, accepted 1 April 1992.*

Migratory stopover sites serve as refueling locations for many migrant passerines, especially those that are physically unable to carry enough fuel (fat) to complete an entire season's migration in one migratory episode (probably most Nearctic-Neotropic passerine migrants; see Berthold 1975; Dawson et al. 1983; Bairlein 1987; Winker et al., in press). Despite the probable importance of stopover sites in the annual life cycles of passerine migrants, very little is known about the demand placed upon the resources at these sites. This ignorance is extensive, existing at local, regional, and continental levels. Broad questions regarding Nearctic-Neotropic passerine migration (e.g., route selection and habitat preferences) remain unanswered. This confounds efforts to understand evolutionary questions regarding these species and may thwart the development of effective conservation policies for migrant populations showing declines (see Robbins et al. 1989, Terborgh 1989).

We believe that a comprehensive picture of Nearctic passerine migration is needed and that many of the data to construct this picture can be obtained only through geographically widespread, multi-year, multi-habitat, single-site banding efforts. Site-specific summary statistics would be very useful in illuminating broad, species-specific aspects of route selection, timing, and habitat preferences. Those data of particular importance in this regard are relative "densities" of birds occurring at a site, structure

[1] Bell Museum of Natural History, 10 Church Street SE, Minneapolis, Minnesota 55455.
[2] Spring Creek Field Laboratory, USDI National Park Service, Marine On St. Croix, Minnesota 55047.

TABLE 1
SEASONAL AND ANNUAL DISTRIBUTIONS OF SAMPLE EFFORT (NET-H)

Year	Net-h-1	
	Spring	Autumn
1984	17,708	22,971
1985	26,667	24,999
1986	27,023	17,829
Total	71,398	65,799

of habitats sampled, some idea of what portion of the migration period was covered by the sample effort, and the median date of individual passage. In this paper we summarize migration at a site in eastern Minnesota and examine our data from local and regional levels.

STUDY AREA AND METHODS

Our study site was located approximately 2 km from the St. Croix River, near Afton, Washington County, Minnesota (44°55′N 92°48′W), in a mosaic of suburban-residential, agricultural, and wooded tracts. Unlike many studies of Nearctic migrants (see refs. in Winker et al. 1992), this site was located far from any ecological barrier to migration (e.g., large body of water, mountains, desert). Our sampling program included five relatively discrete wooded habitat patches which ranged in size from approximately 1–3+ ha. These habitats, representative of the area's native woodlands, were called Floodplain, Swamp, Upland, Willows, and Oaks. Upland and Oaks were well-drained sites; Swamp, Floodplain, and Willows were moister (with occasional shallow pools of surface water) and were close to Valley Creek, a small stream flowing through the site.

Standard mist nets (12 m × 2.6 m of 30- and 36-mm mesh) were placed 30 m apart along lines that were themselves 30 m apart. The ends of the nets were pointed E and W, enabling the capture of birds moving N or S. The number of nets in each habitat varied according to patch size: Floodplain (18), Swamp (12), Upland (18), Willows (12), and Oaks (10). Nocturnal captures were rare, and nets were closed only for inclement weather or personnel limitations. Sample effort (mist net hours, or net-h) was recorded daily; on days when nets were not closed, net-h were calculated as sunrise-to-sunset time plus 0.5 h. The specific net of capture was among the data recorded for every captured bird. Nets were operated 1–27 May and 9 Aug.–24 Sept. 1984, 29 Apr.–29 May and 14 Aug.–22 Sept. 1985, and 28 Apr.–28 May and 17 Aug.–23 Sept. 1986. Thus, our overall sample effort spanned 32 days in spring (Julian days 118–149) and 47 days in autumn (Julian days 222–268). The distribution of sample effort varied seasonally and annually (Table 1). Analyses of habitat distribution employ data from days on which the habitats considered were sampled simultaneously (see Winker et al., in press, for more details).

The vegetative structure and composition of each habitat (Appendix) was measured using the method of James and Shugart (1970) with slight modifications. We centered our examinations on the center of each net lane, measuring the vegetation in two semicircles (11.35 m radius) separated by 2 m (total area 0.04 ha). This effectively removed the bare, 1.5–2 m net lane from consideration. We also used a range-finder for increased accuracy in de-

termining the limits of the 11.35 m radius. Shrub taxa were included, and we present those which comprised 90% of the total shrub stem count. All net locations were sampled, thus our minimum sample in any habitat was ten 0.04-ha circles (Oaks), which is twice the minimum number recommended by James and Shugart (1970). Because nets were placed on a 30 m grid, we consider that tree analysis directly measured approximately 50% of the area our nets were placed to sample, and that shrub analysis directly measured approximately 5% of the same area.

RESULTS

During six seasons of netting we captured 17,019 birds of 100 species. These figures alone suggest substantial use of these small wooded patches by transient migrants. Evidence considered elsewhere suggests that migrants at our site were feeding—some on an impressive scale (Winker et al., in press, unpubl. data). Resources at this site were used by migrants for fattening in spring and for fattening and molting in autumn (molt occurred among transient as well as locally breeding species; Winker et al. 1991, in press, unpubl. data). When examined on a seasonal basis, capture rates varied considerably among years (Table 2). Much of this variation was no doubt due to weather variability. Eight of the 100 species encountered at our site during migration were permanent residents, and these species made up 5.2% of the total individuals captured. Of the 92 species of migrants, 69 species were represented by 10 or more individuals (Table 2). Of these 69 migrant species 58 (84%) were Nearctic-Neotropic migrants (after Rappole et al. 1983:108).

Timing.—Our netting periods spanned the bulk of both spring and autumn migration (Fig. 1), but did not encompass the full migratory periods of several species, most of which were Nearctic-Neotropic migrants (unpubl.). An examination of individual passage through time (Fig. 1, unpubl.) reveals that the largest numbers of birds occurred at our site near the middle of our netting periods. Analyses of median passage times suggest that peak resource demands (as reflected in numbers of birds present) occurred in the days surrounding 14 May (Julian day 134) and 31 Aug. (Julian day 243) which are the median dates of passage for the combination of all individuals of migrant species in Table 2.

Elsewhere (Winker et al., in press), we found that the availability of median date information in the literature allowed us to examine the speed of northward passage in Swainson's Thrush in spring. Although spring passage has received much attention, autumn passage data are largely nonexistent for most migrant species. Here we present both spring and autumn median passage data for many of the migrants at our site (Table 2), hoping that others will find them useful for making geographic comparisons. Four species showed a difference between spring and autumn median passage at our site of 95 days or less: the Yellow-bellied Flycatcher,

TABLE 2

SUMMARY OF CAPTURES BY SEASON (1984–1986) FOR SPECIES REPRESENTED BY MORE THAN 10 INDIVIDUALS. RECAPTURES ARE EXCLUDED. RESIDENT SPECIES ARE INCLUDED TO PORTRAY LOCAL COMMUNITY STRUCTURE AND TO ALLOW RELATIVE ABUNDANCE ESTIMATES. MEDIAN DATES OF OCCURRENCE ARE NOT GIVEN FOR RESIDENT SPECIES, NOR FOR MIGRANT SPECIES WHOSE SEASONAL MOVEMENTS WERE NOT ADEQUATELY ENCOMPASSED BY OUR SAMPLE PERIODS

		SPRING[a]				AUTUMN[b]			
Species	Status[c]	N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]	N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]
American Woodcock (*Scolopax minor*)	M	8	121–147	—	0.11 (0.06–0.16)	6	233–264	—	0.09 (0.06–0.12)
Ruby-throated Hummingbird (*Archilochus colubris*)	M	86	128–148	140	1.22 (0.34–2.26)	387	227–265	241	5.88 (5.05–7.04)
Red-bellied Woodpecker (*Melanerpes carolinus*)	R	5	122–135	—	0.07 (0.04–0.11)	7	234–267	—	0.11 (0.06–0.16)
Downy Woodpecker (*Picoides pubescens*)	R	45	118–148	—	0.64 (0.30–1.58)	105	226–266	—	1.60 (1.18–1.88)
Hairy Woodpecker (*P. villosus*)	R	21	121–135	—	0.30 (0.04–0.73)	30	227–262	—	0.46 (0.30–0.60)
Yellow-shafted Flicker (*Colaptes a. auratus*)	M	2	132–142	—	0.03 (0.00–0.06)	8	231–264	—	0.12 (0.04–0.22)
Olive-sided Flycatcher (*Contopus borealis*)	T	2	135–140	—	0.03 (0.00–0.06)	52	229–251	241	0.81 (0.64–1.23)
Eastern Wood-Pewee (*C. virens*)	M	8	137–147	142–3	0.11 (0.00–0.34)	97	229–264	243	1.47 (1.23–1.68)
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	T	28	138–148	146	0.40 (0.11–0.96)	236	229–264	240	3.59 (1.74–4.66)
"Traill's" Flycatcher (*E. "traillii"* spp.)	T	41	125–149	143	0.67 (0.37–1.52)	207	229–264	240	3.15 (2.00–4.21)
Least Flycatcher (*E. minimus*)	T	326	118–148	133	4.36 (1.11–13.78)	153	229–265	242	2.33 (1.39–3.16)

TABLE 2
CONTINUED

Species	Status[c]	SPRING[a] N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]	AUTUMN[b] N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]
Eastern Phoebe (*Sayornis phoebe*)	M	4	119–138	—	0.06 (0.00–0.12)	21	232–266	247	0.32 (0.17–0.45)
Great Crested Flycatcher (*Myiarchus crinitus*)	M	14	127–147	140	0.20 (0.00–0.51)	34	227–262	235–6	0.52 (0.13–0.80)
Blue Jay (*Cyanocitta cristata*)	R	24	121–147	—	0.34 (0.19–0.62)	31	230–267	—	0.47 (0.26—0.80)
Black-capped Chickadee (*Parus atricapillus*)	R	134	118–147	—	1.90 (1.01–4.12)	325	222–267	—	4.94 (4.22–5.84)
Red-breasted Nuthatch (*Sitta canadensis*)	T	7	119–138	—	0.10 (0.04–0.28)	35	235–265	—	0.53 (0.00–1.40)
White-breasted Nuthatch (*S. carolinensis*)	R	35	120–147	—	0.50 (0.23–1.19)	42	226–265	—	0.64 (0.45–0.88)
Brown Creeper (*Certhia americana*)	T	9	122–134	—	0.13 (0.00–0.51)	27	242–267	—	0.41 (0.30–0.48)
House Wren (*Troglodytes aedon*)	M	95	118–148	—	1.35 (1.15–1.58)	105	226–266	238	1.60 (0.56–2.32)
Winter Wren (*T. troglodytes*)	T	3	118–123	—	0.04 (0.00–0.11)	40	248–267	—	0.62 (0.56–0.68)
Golden-crowned Kinglet (*Regulus satrapa*)	T	0	—	—	— —	10	255–265	—	0.15 (0.00–0.32)
Ruby-crowned Kinglet (*R. calendula*)	T	241	118–139	—	3.42 (0.78–8.30)	97	243–267	—	1.47 (1.24–1.85)
Blue-gray Gnatcatcher (*Polioptila caerulea*)	M	10	118–147	134–5	0.14 (0.00–0.23)	6	229–244	—	0.09 (0.00–0.20)
Veery (*Catharus fuscescens*)	T	45	120–146	136	0.64 (0.37–1.41)	67	229–267	243	1.02 (0.26–1.51)
Gray-cheeked Thrush (*C. minimus*)	T	149	124–148	132	2.11 (0.93–5.14)	48	238–265	256-7	0.73 (0.30–1.16)

TABLE 2
CONTINUED

Species	Status[c]	SPRING[a] N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]	AUTUMN[b] N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]
Swainson's Thrush (*C. ustulatus*)	T	347	119–148	138	4.91 (1.81–12.65)	663	229–267	254	10.08 (5.01–14.36)
Hermit Thrush (*C. guttatus*)	T	12	119–137	—	0.17 (0.04–0.34)	3	232–264	—	0.05 (0.00–0.08)
Wood Thrush (*Hylocichla mustelina*)	M	43	125–147	139	0.61 (0.30–1.41)	31	231–266	251	0.47 (0.11–0.83)
American Robin (*Turdus migratorius*)	M	38	118–147	—	0.54 (0.35–0.70)	53	229–266	—	0.81 (0.60–1.13)
Gray Catbird (*Dumetella carolinensis*)	M	233	125–148	139	3.31 (2.60–5.99)	401	222–267	—	6.11 (5.72–6.44)
Cedar Waxwing (*Bombycilla cedrorum*)	M	291	119–148	—	4.13 (0.97–7.51)	136	229–266	—	2.07 (1.61–3.25)
Solitary Vireo (*Vireo solitarius*)	T	99	122–145	133	1.41 (0.04–5.31)	137	233–267	255	2.08 (1.96–2.19)
Yellow-throated Vireo (*V. flavifrons*)	T	0	—	—	— —	13	230–266	242	0.20 (0.04–0.32)
Warbling Vireo (*V. gilvus*)	T	10	127–146	140	0.14 (0.00–0.51)	12	235–263	244	0.18 (0.11–0.26)
Philadelphia Vireo (*V. philadelphicus*)	T	11	127–145	135	0.16 (0.04–0.40)	166	230–266	249	2.52 (2.05–3.65)
Red-eyed Vireo (*V. olivaceus*)	M	37	130–148	142	0.53 (0.19–1.47)	745	229–267	243	11.32 (4.96–15.52)
Blue-winged Warbler (*Vermivora pinus*)	M	24	127–146	134-5	0.34 (0.19–0.73)	8	229–250	236	0.12 (0.11–0.13)
Golden-winged Warbler (*V. chrysoptera*)	T	12	127–140	135	0.17 (0.07–0.34)	46	234–263	244	0.70 (0.56–0.90)
Tennessee Warbler (*V. peregrina*)	T	38	127–144	134	0.54 (0.31–0.68)	777	226–266	240	11.81 (3.48–18.88)

TABLE 2
CONTINUED

Species	Status[c]	SPRING[a] N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]	AUTUMN[b] N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]
Orange-crowned Warbler (*V. celata*)	T	48	118–135	—	0.68 (0.51–1.07)	11	251–266	—	0.18 (0.04–0.35)
Nashville Warbler (*V. ruficapilla*)	T	143	120–147	134	2.03 (0.89–3.84)	715	229–267	248	10.93 (9.84–12.16)
Northern Parula (*Parula americana*)	T	0	—	—	— —	13	239–253	249	0.20 (0.08–0.35)
Yellow Warbler (*Dendroica petechia*)	T	26	124–147	135	0.37 (0.07–0.96)	3	230–244	—	0.05 (0.00–0.08)
Chestnut-sided Warbler (*D. pensylvanica*)	T	31	130–147	138	0.44 (0.30–0.56)	386	229–267	242	5.87 (3.70–8.76)
Magnolia Warbler (*D. magnolia*)	T	105	126–149	137	1.49 (0.70–3.73)	778	229–267	242	11.84 (5.53–18.40)
Cape May Warbler (*D. tigrina*)	T	0	—	—	— —	47	229–262	238	0.71 (0.00–1.20)
Black-throated Blue Warbler (*D. caerulescens*)	T	0	—	—	— —	11	240–261	252	0.17 (0.13–0.22)
Myrtle Warbler (*D. c. coronata*)	T	84	118–135	—	1.19 (0.19–2.94)	15	229–266	—	0.23 (0.08–0.45)
Black-throated Green Warbler (*D. virens*)	T	7	132–137	135	0.10 (0.00–0.28)	82	233–264	244	1.25 (1.16–1.40)
Blackburnian Warbler (*D. fusca*)	T	3	135–145	—	0.04 (0.00–0.11)	57	229–265	242	0.87 (0.44–1.44)
Western Palm Warbler (*D. p. palmarum*)	T	15	118–133	—	0.21 (0.12–0.30)	3	250–263	—	0.05 (0.00–0.12)
Bay-breasted Warbler (*D. castanea*)	T	0	—	—	— —	184	229–266	245	2.80 (1.52–3.93)

TABLE 2
CONTINUED

Species	Status[c]	SPRING[a] N	SPRING[a] Date range[d]	SPRING[a] Median	SPRING[a] Mean birds/1000 net-h (Range)[e]	AUTUMN[b] N	AUTUMN[b] Date range[d]	AUTUMN[b] Median	AUTUMN[b] Mean birds/1000 net-h (Range)[e]
Blackpoll Warbler (*D. striata*)	T	8	135–138	136-7	0.11 (0.00–0.45)	7	249–261	255	0.11 (0.00–0.39)
Black-and-white Warbler (*Mniotilta varia*)	T	84	125–146	133	1.19 (0.07–4.01)	275	226–265	242	4.19 (1.78–6.64)
American Redstart (*Setophaga ruticilla*)	T	94	125–148	139-40	1.33 (0.52–3.11)	527	229–267	242	8.01 (5.49–11.36)
Ovenbird (*Seiurus aurocapillus*)	M	165	120–148	135	2.34 (1.63–4.35)	658	229–267	247	10.03 (6.79–13.76)
Northern Waterthrush (*S. noveboracensis*)	T	431	118–148	132	6.12 (3.48–9.88)	234	227–265	245	3.57 (3.35–4.04)
Connecticut Warbler (*Oporornis agilis*)	T	4	141–146	—	0.06 (0.00–0.17)	47	230–263	243	0.71 (0.44–1.00)
Mourning Warbler (*O. philadelphia*)	T	88	135–148	142-3	1.25 (0.67–2.03)	124	230–264	242	1.88 (1.26–2.84)
Common Yellowthroat (*Geothlypis trichas*)	M	245	121–148	139	3.48 (2.00–6.55)	217	222–267	242	3.30 (2.64–4.09)
Wilson's Warbler (*Wilsonia pusilla*)	T	119	126–147	138	1.69 (0.41–4.57)	158	229–264	243	2.40 (1.35–3.28)
Canada Warbler (*W. canadensis*)	T	45	124–148	145	0.64 (0.37–1.07)	222	229–266	240	3.37 (1.92–4.16)
Scarlet Tanager (*Piranga olivacea*)	M	17	134–148	140	0.24 (0.00–0.79)	21	233–267	245	0.35 (0.00–0.57)
Northern Cardinal (*Cardinalis cardinalis*)	R	59	118–148	—	0.84 (0.81–0.90)	23	230–264	—	0.35 (0.17–0.44)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	M	83	125–148	135	1.18 (0.70–2.43)	261	226–267	244	3.98 (3.81–4.09)

TABLE 2
CONTINUED

Species	Status[c]	SPRING[a] N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]	AUTUMN[b] N	Date range[d]	Median	Mean birds/1000 net-h (Range)[e]
Indigo Bunting (*Passerina cyanea*)	M	72	125–149	142	1.02 (0.78–1.40)	43	226–265	236	0.65 (0.06–1.35)
Chipping Sparrow (*Spizella passerina*)	M	32	121–149	—	0.45 (0.15–1.02)	3	237–249	—	0.05 (0.00–0.12)
Field Sparrow (*S. pusilla*)	M	5	121–141	—	0.07 (0.06–0.08)	10	235–267	—	0.15 (0.00–0.39)
Song Sparrow (*Melospiza melodia*)	M	58	118–148	—	0.82 (0.79–0.86)	122	222–264	—	1.85 (1.40–2.13)
Lincoln's Sparrow (*M. lincolnii*)	T	32	122–146	131-2	0.45 (0.11–0.90)	15	250–267	—	0.26 (0.00–0.57)
Swamp Sparrow (*M. georgiana*)	T	138	118–145	126	1.96 (0.89–4.91)	13	250–265	—	0.20 (0.00–0.56)
White-throated Sparrow (*Zonotrichia albicollis*)	T	224	118–141	—	3.18 (1.59–6.32)	155	229–267	—	2.40 (1.48–3.87)
Brown-headed Cowbird (*Molothrus ater*)	M	12	127–148	—	0.17 (0.08–0.34)	0	—	—	— —
Baltimore Oriole (*Icterus g. galbula*)	M	22	133–149	140-1	0.31 (0.11–0.90)	20	230–244	237	0.30 (0.00–0.48)
Purple Finch (*Carpodacus purpureus*)	T	3	122–128	—	0.04 (0.00–0.07)	203	231–264	—	3.09 (0.26–4.68)
Pine Siskin (*Carduelis pinus*)	M	21	119–145	—	0.30 (0.04–0.79)	9	249–259	—	0.14 (0.00–0.50)
American Goldfinch (*C. tristis*)	M	132	121–148	—	1.87 (1.30–2.76)	686	226–267	—	10.43 (2.75–24.47)

[a] Includes days 118–149.
[b] Includes days 222–268.
[c] Species' status at our site. M = migrant species with resident breeding populations; R = resident species; T = transient species (in some cases the species is known to breed in the region, but our site did not have a breeding population).
[d] Earliest and latest Julian dates of capture within the particular season.
[e] Average capture rates over all three years expressed as birds per 1000 net-h. "Range" shows minimum and maximum annual rates.

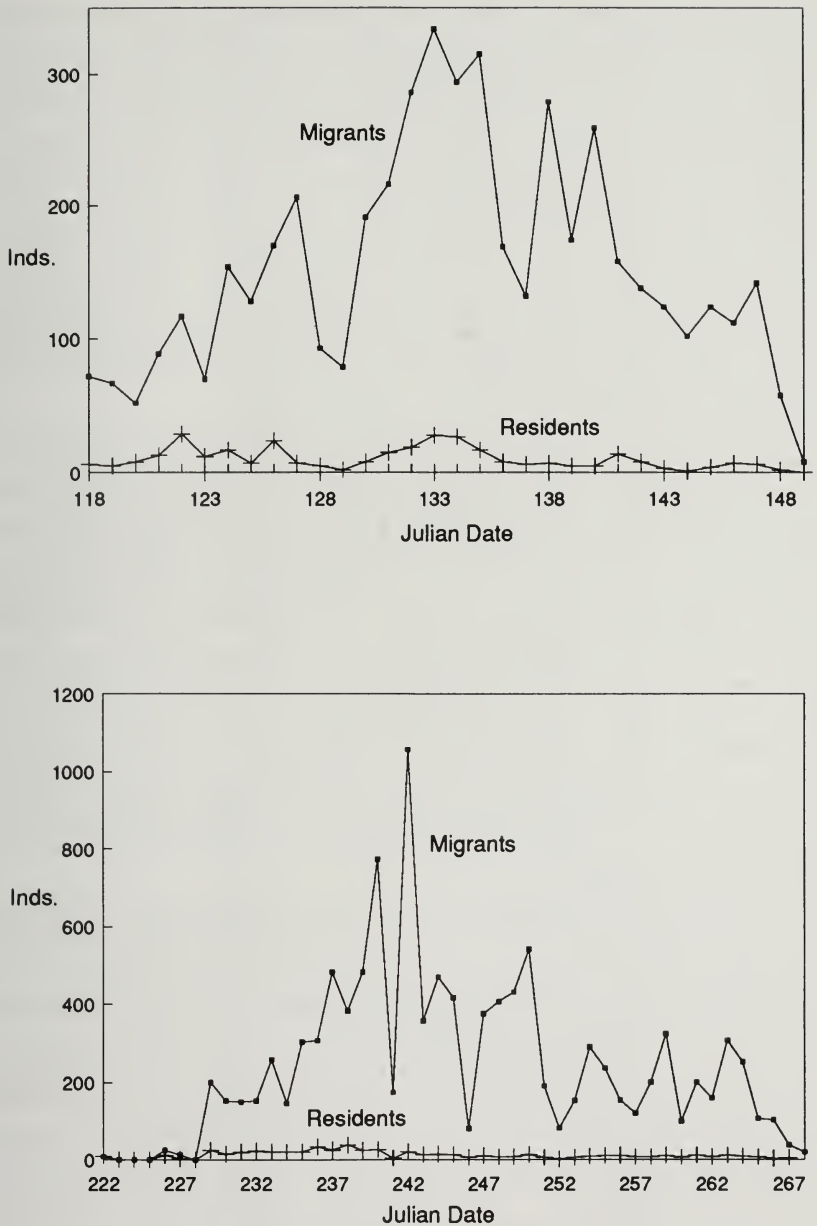

FIG. 1. Total number of birds captured by Julian day during spring (top) and autumn (bottom), 1984–1986. In non-leap years, 15 May = Day 135 and 1 September = Day 244.

Least Flycatcher, Canada Warbler, and Indigo Bunting (scientific names in Table 2). Three-quarters or more of the annual life cycles of the populations of these species that we sampled are thus spent away from the breeding grounds. The Yellow-bellied and Least flycatchers have been shown elsewhere to spend very little time on their breeding grounds; in both species the adults undergo flight feather molt on the wintering grounds following autumn migration (Hussell 1981, 1982). Eighteen of the migrant species in Table 2 showed a difference between median spring and autumn passage of 105 days or less (counting the *Empidonax* "*traillii*" complex as one species). Thus, about 53% of those migrant species whose seasonal movements were adequately encompassed by our sample periods spend less than 30% of their annual life cycles on their breeding grounds. All of these species are Nearctic-Neotropic migrants (Table 2).

Route selection.—If migrants proceeded directly north in spring, reproduced on their breeding grounds, and returned directly south, captures at a single stopover site would show (on average) more birds (higher capture rates) in autumn than in spring due to the production of young. Although we know that seasonal movements are not so simplistic (e.g., see Rappole et al. 1979), in general migrants at our site showed this predicted relationship (Tables 2 and 3). Several species departed from this trend, however, suggesting that they use different migratory routes. Those species adequately encompassed by our study period that showed greater capture rates in spring than autumn were the Least Flycatcher, Gray-cheeked Thrush, Blue-winged Warbler, Yellow Warbler, Northern Waterthrush, Common Yellowthroat, and Indigo Bunting (Table 2). Relationships of this nature are expected if routes shift seasonally and the banding site lies in a zone near an edge of the autumn route, but well within the spring route.

Several species were not captured at our site in spring, but were captured in autumn: Yellow-throated Vireo, Northern Parula, Cape May Warbler, Black-throated Blue Warbler, and Bay-breasted Warbler (Table 2). This relationship is expected when the site lies outside (or nearly outside) the spring route, but somewhere within the autumn route. Although we say "the" autumn or spring route, we are aware that migration can differ in timing and route selection for sex, age, and population groups (see Phillips 1951, Ramos 1988). We are concerned here, however, with broad, species-level questions, which remain poorly understood (see, for example, Hussell 1980 vs Rappole et al. 1979 and Murray 1989 vs other authors for conflicting hypotheses concerning autumn routes of the Least Flycatcher and Blackpoll Warbler, respectively).

If our sampled habitats were not adequately diverse, a seasonal habitat preference shift could cause fewer captures in autumn, affecting our con-

TABLE 3

DISTRIBUTIONS OF MEAN CAPTURE RATES AMONG HABITATS ON DAYS OF SIMULTANEOUS SAMPLING (RECAPTURES EXCLUDED, ALL YEARS INCLUDED). THE TOP HALF OF THE TABLE COMPARES THE FOUR MOST THOROUGHLY STUDIED HABITATS, WHILE THE LOWER HALF INCLUDES THE LESS STUDIED FIFTH (OAKS)

		Capture rates (SD)[b]						
Season	N^a	Swamp	Floodplain	Willow	Upland		F	P
Spring	70	126.1 (107.7)	84.4 (71.0)	56.2 (60.3)	25.6 (36.5)		23.69	<0.00005
Autumn	57	347.7 (303.8)	203.8 (225.4)	91.7 (95.7)	50.0 (60.8)		25.92	<0.00005
		Swamp	Floodplain	Willow	Oaks	Upland		
Spring	33	134.5 (129.0)	91.9 (89.4)	71.5 (73.8)	66.9 (89.0)	27.3 (44.0)	6.32	0.0001
Autumn	23	403.5 (418.5)	245.9 (327.8)	108.3 (131.7)	167.0 (191.6)	65.1 (85.8)	5.95	0.0002

[a] Number of days on which habitats considered were sampled simultaneously.
[b] Birds per 1000 net-h, recaptures excluded.
[c] Members of underscored groups are not significantly different from one another; different underscorings represent groups significantly different from one another at the 0.05 level (ANOVA).

clusions regarding species showing apparent seasonal route differences. Our selection of habitats, however, encompassed the wooded types available, and we feel that this factor did not cause the majority of the observed abundance anomalies. The idea that a "narrow" array of sampled habitats caused seasonal differences in capture rates has the most plausibility for the Common Yellowthroat (a species not strictly associated with woodlands), but Floodplain and Swamp had dense breeding populations of this species, so habitat suitable for breeding (at least) was sampled.

The Least Flycatcher, Common Yellowthroat, and Indigo Bunting were inconsistent from year to year in relative seasonal abundance, perhaps a weather-related phenomenon (unpubl.). Blue-winged and Yellow warblers were relatively uncommon at our site (Table 2). In addition, the latter is an early autumn migrant (Janssen 1987). Ely (1970) found the Least Flycatcher to be more common in spring than autumn in west-central Kansas, and the expected "greater in autumn" capture rates occur in western Pennsylvania (Clench and Leberman 1978). These relationships are consistent with the route for this species proposed by Rappole et al. (1979:210, Route 5), wherein the spring route lies generally west of the autumn (primarily trans-Gulf) route. Northern populations of the Indigo Bunting may follow a narrower autumn route that falls within a wider spring route, as suggested by more encounters in spring than autumn both at our site and at Powdermill in western Pennsylvania (Clench and Leberman 1978; see also Ralph 1981). Further south, this species may follow a route similar to that of the Least Flycatcher, but with a more pronounced eastward trend over the Gulf of México and southern Florida (see data in Rappole and Warner 1976, Crawford 1981).

The Northern Waterthrush and Gray-cheeked Thrush showed consistent seasonal abundance imbalances (unpubl.), and the two species may follow similar routes. Rappole et al. (1979:203) considered that both species followed an easterly, primarily trans-Gulf autumn route, although we note that both species occur in both seasons in southern Florida (Crawford 1981). Our data suggest that the eastwardly autumn trend in both species begins far north of the Gulf of México, although western populations of the Northern Waterthrush probably follow a different route (cf Grinnell 1915, Phillips et al. 1964, Oberholser 1974:773).

Two of the five species noted above that were not captured in spring but which appeared in autumn showed a high percentage of young birds in the overall sample, a factor which Ralph (1981) considered an edge-of-route phenomenon (often encountered in coastal areas). In the Cape May and Black-throated Blue warblers, immatures made up 89% and 91%, respectively, of the autumn captures (N = 47 and 11; Table 2), suggesting that our site might fall along the western edge of these species'

autumn routes in our region. Janssen (1987) suggested that the Black-throated Blue Warbler arrives and departs the state from the east; our data imply that this species and the Cape May might follow similar regional routes, with a large east-west component, but with either a widening of the autumn route or a stronger southward autumn component. The same general conclusion might also apply to the Northern Parula and Bay-breasted Warbler. However, the lower average immature composition (Northern Parula: 69.2%, N = 13; Bay-breasted Warbler: 75.5%, N = 184), suggests that our site lies further within the autumn routes of these species than those of the previous two. This conclusion is particularly relevant to the Bay-breasted Warbler, given its autumn abundance at our site. Unlike the previous four species, the Yellow-throated Vireo breeds in areas near our site (Janssen 1987), and in spring our nets failed to capture individuals known to be present as transients (pers. obs.). Thus, without further data we cannot determine whether this species shows seasonal route shifts in relation to our site or whether it is typical of the majority of species: simply more common in autumn than in spring.

Habitat selection.—Standard mist nets can only sample a vertical stratum of about 2.5 m. Interpretations of capture rates between habitats with different canopy heights must therefore consider that different percentages of the vegetative stratum have been sampled in each habitat. For ground-foraging species this is not a problem, but most of the species captured at our site forage (at aboveground or near-ground levels). Our average capture rates in each habitat do show a strong relationship with mean canopy height (Table 3, Appendix), so we cannot determine which habitat(s) are preferred overall. It is clear, however, that seasonal changes in distribution do occur at our site (Table 3). These differences are due to disproportionate increases in capture rates between spring and autumn in each habitat. In general, a greater percentage of the overall autumn increase at our site occurred in the Swamp and Floodplain than in the other three habitats. If we consider the four habitats netted most thoroughly (and in parentheses the lesser number of days upon which all five habitats were sampled simultaneously; both from Table 3), average spring capture rates represented a varying percentage of average autumn capture rates for each habitat: Swamp 36.2% (33.3%), Floodplain 41.4% (37.4%), Willows 61.3% (66.0%), Upland 51.2% (41.9%), and Oaks (40.0%).

Are measured habitat variables correlated with the observed seasonal shifts in distribution? The high variability of daily capture rates (see standard deviations, Table 3) makes it difficult to assess possible correlations between seasonal increases in capture rates (above) and habitat-related parameters (Appendix). Individuals of the more common migrant species at our site were captured in most, if not all, of the habitats sampled

(unpubl.). Of the woody vegetation, only two shrub taxa were shared as a common feature among the five sampled habitats: dogwoods (*Cornus* spp.) and buckthorn (*Rhamnus catharticus*), an exotic species common at our site (Appendix). The seasonal increases in capture rates showed no relationship to dogwood densities, but may be related to buckthorn densities. The habitat showing the least increase in autumn captures (Willows) has the highest density of buckthorn, and that with the greatest autumn increase (Swamp) has the lowest density of this species (visual examination of mean capture rates vs mean buckthorn densities). The meaning of this relationship requires a more detailed analysis (net-by-net) than we can present here.

Swamp and Floodplain were the wettest of the five habitats (not quantified), and also had the greatest ground cover and least canopy cover (Appendix). These habitats showed the highest increases in capture rates between spring and autumn. The disproportionate seasonal capture rate increases do not appear to be related to canopy height or any of the other four measured structural characteristics. Thus, if foraging height does not change seasonally in a habitat-specific manner (something we cannot address), our data suggest that the avian community as a whole undergoes a seasonal shift in habitat use at this site.

DISCUSSION

It is impossible to estimate what percentage of birds occurring in a habitat are captured, but it is clear (Fig. 1) that our small forested patches were used by a considerable number of migrants during our study. This occurrence, together with our finding that a seasonal spatial shift in distribution occurs among these habitats, suggests that a diverse array of forest fragments may serve an important role to stopover migrants. No habitat at our site could be singled out as being "best" for woodland-associated migrants. The coincidence of median dates among many species (Table 2), the numbers of birds present, and the relatively short period of time in which migration occurs (Table 2, Fig. 1) suggest that seasonal demand on the resources at this site is acute. Several decades of invertebrate abundance data for deciduous woods approximately 680 km SE of our site show two pronounced annual peaks, occurring in May and September (Kendeigh 1979:35), suggesting that Nearctic deciduous woodlands may have higher levels of invertebrate food resources available during migrant passage than at other times of the year. Further data (and better geographic concordance) would be required to determine whether the timing of migration in the species considered here is affected by the availability of food at potential stopover sites.

Demonstrations of seasonal shifts in habitat use by migrant passerines are rare (Jones 1895; Hutto 1985; Winker et al. 1992), but this may be because they have not been looked for. We are not aware of another study that has demonstrated a seasonal spatial shift in the avian community as a whole at a stopover site. The seasonal shifts in the distribution of capture rates among our sampled habitats (Table 3) are of a somewhat uncertain nature, because habitats of different canopy heights are not equivalently sampled by mist nets. While these analyses show that some spatial shifts occurred, we cannot determine whether these changes were caused by two-dimensional shifts (seasonal changes in habitat use) or three-dimensional shifts (seasonally different foraging levels causing different capture susceptibilities among habitats with variable canopy heights). The lack of correlation between relative seasonal increases in capture rates and canopy height suggests that two-dimensional shifts are a more important factor. We know that for at least two ground or near-ground level foragers (Swainson's Thrush and the Northern Waterthrush), two-dimensional shifts are occurring (Winker et al. 1992), although neither of the patterns of seasonal change shown by these common species matches that of the overall avian community. The seasonal changes in distribution shown at our site could be caused by seasonal changes in habitat use alone or in combination with seasonal shifts in foraging heights.

The eastward trends in autumn migration noted for the Northern Waterthrush and Gray-cheeked Thrush raise questions. *Why* such an eastward swing should occur well north of the nearest ecological barrier (Gulf of México) in only two of the species encountered commonly at our site will likely remain a mystery until we can discover more about the movements of these species and others with similar (and dissimilar) breeding and wintering ranges.

When placed across a variety of available habitats, mist nets allow a quantification of migrant abundance, timing, and habitat preference(s) at a stopover site. Summary statistics from these sites are few, but, as shown here, can be useful in illuminating local and regional patterns of passerine migration. Only when such summaries are available across a broader geographic area can we hope to understand specific migration strategies at the regional and continental levels.

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Appendix I

Vegetative Structure and Composition of Each Sampled Habitat

Primer.—Species of trees: Figures after each give number of trees/ha, relative density (%), relative dominance (%), and frequency of sample circles at which species occurred (%), in that sequence. Size class information: Tree diameter size classes are as follows (conversion directly from inches-based methodology allows direct comparison to an established literature base): *A* (7.6–15.2 cm), *B* (15.2–22.9 cm), *C* (22.9–38.1 cm), *D* (38.1–53.3 cm), *E* (53.3–68.6 cm), and *F* (68.6–83.8 cm). Figures after each size class give number of trees/ha of that class, relative density (%), basal area (m^2/ha), and relative dominance (%). Shrubs by taxon: Figures after each give relative density (%) and frequency of circles at which taxon occurred (%).

1. *Floodplain.*—Trees 7.6 cm diameter and over, 443/ha; total basal area, 16.5 m^2/ha. Species comprising 90% of the total number of trees: *Salix nigra,* 186.9, 42.2, 66.9, 100; *Ulmus americana,* 99.5, 22.5, 10.5, 92; *Acer saccharinum,* 92.4, 20.9, 11.6, 62.5; *Acer negundo,* 22.1, 5.0, 1.5, 25. Trees by diameter size class: *A* 160.8, 36.3, 1.5, 9; *B* 165.8, 37.4, 4.6, 28; *C* 100.5, 23.7, 7.5, 45; *D* 14.1, 3.2, 2.4, 14.3; *E* 2.0, 0.5, 0.6, 3.5. Shrub stems/ha, 18,430 (est.). Shrub taxa comprising 90% of the total number of shrubs: *Rhamnus catharticus,* 38.6, 95.8; *Cornus* spp., 31.9, 100; *Alnus rugosa,* 10.0, 41.7; *Salix* sp., 5.7, 45.8; *Acer negundo,* 3.1, 75. Ground cover, 88%; canopy cover, 50%; mean canopy height, 13.1 m (range 4.6–18.3 m).

2. *Swamp.*—Trees 7.6 cm diameter and over, 53/ha; total basal area, 1.2 m^2/ha. Species comprising 90% of the total number of trees: *Ulmus americana,* 18.1, 34.6, 21, 33.3; *Betula papyrifera,* 16.1, 30.8, 29, 16.6; *Salix nigra,* 10.1, 19.2, 40.3, 25; *Populus tremuloides,* 4, 7.7, 6.5, 8.3; *Acer saccharinum,* 2, 3.9, 1.6, 8.3. Trees by diameter size class: *A* 26.1, 41.7, 0.2, 21; *B* 22.1, 35.3, 0.6, 53.2; *C* 4, 6.4, 0.3, 25.8. Shrub stems/ha, 20,052 (est.). Shrub taxa comprising 90% of the total number of shrubs: *Alnus rugosa,* 36.4, 91.7; *Cornus* spp., 21.2, 100; *Betula pumila,* 13.3, 50; *Salix* sp., 12.8, 100; *Rhamnus catharticus,* 8, 58.3. Ground cover, 90.8%; canopy cover, 20%; mean canopy height, 4.8 m (range 1.5–9.1 m).

3. *Upland.*—Trees 7.6 cm diameter and over, 729/ha; total basal area, 24.6 m^2/ha. Species comprising 90% of the total number of trees: *Populus tremuloides,* 198.2, 27.2, 18.8, 44.4; *Quercus alba,* 158.2, 21.7, 35.3, 72.2; *Betula papyrifera,* 124.6, 17.1, 12.8, 72.2; *Tilia americana,* 65.6, 9, 5.8, 83.3; *Quercus rubra,* 53.5, 7.4, 15.4, 66.7; *Prunus serotina,* 33.5, 4.6, 4.2, 66.7; *Ostrya virginiana,* 26.8, 3.7, 1.1, 27.8. Trees by diameter size class: *A* 304, 41.7, 2.8, 11.5; *B* 262.6, 36, 7.3, 29.8; *C* 136.7, 18.8, 10.1, 41.4; *D* 25.6, 3.5, 4.3, 17.3. Shrub stems/ha, 4561 (est.). Shrub taxa comprising 90% of the total number of shrubs: *Rhamnus catharticus,* 34.9, 100; *Tilia americana,* 16.6, 83.3; *Prunus* spp., 11.5, 61.1; *Cornus* spp., 9.5, 55.6; *Acer negundo,* 8.8, 88.9; *Ostria virginiana,* 5.9, 38.9; *Populus* spp., 2.79, 27.8. Ground cover, 61.4%; canopy cover, 83.1%; mean canopy height, 16.8 m (range 13.7–21.3 m).

4. *Willows.*—Trees 7.6 cm diameter and over, 553/ha; total basal area, 24.3 m^2/ha. Species comprising 90% of the total number of trees: *Populus tremuloides,* 154.7, 28, 14.9, 75; *Salix nigra,* 102.5, 18.6, 56.4, 41.7; *Acer saccharinum,* 92.4, 16.7, 9.3, 58.3; *Prunus virginiana,* 58.3, 10.6, 4.9, 33.3; *Ulmus americana,* 40.2, 7.3, 2.5, 50; *Acer negundo,* 30.1, 5.5, 2.2, 50; *Quercus rubra,* 22.1, 4, 3.2, 50. Trees by diameter size class: *A* 248.3, 85.8, 1.9, 7.9; *B* 255.6, 88.3, 5.9, 24.5; *C* 91.6, 31.7, 5.7, 23.4; *D* 57.9, 20, 8.1, 33.3, *E* 7.2, 2.5, 1.7, 7.2; *F* 2.4, 0.8, 0.9, 3.8. Shrub stems/ha, 21,388 (est.). Shrub taxa comprising 90% of the total number of shrubs: *Rhamnus catharticus,* 58.2, 100; *Cornus* sp., 12.6, 83.3; *Ribes* spp., 9.53, 75; *Corylus* sp., 4.7, 58.3; *Ulmus americana,* 3.3, 100; *Acer negundo,* 3.1, 75. Ground cover, 70.4%; canopy cover, 68.3%; mean canopy height, 15.2 m (range 12.2–21.3 m).

5. *Oaks.*—Trees 7.6 cm diameter and over, 581/ha; total basal area, 24.6 m^2/ha. Species comprising 90% of the total number of trees: *Quercus macrocarpa,* 306.2, 52.7, 42.7, 100; *Quercus rubra,* 178.4, 30.1, 48.2, 90; *Prunus serotina,* 36.2, 6.2, 1.9, 50; *Populus tremuloides,* 21.7, 3.7, 3.5, 20. Trees by diameter size class: *A* 159.1, 27.4, 1.5, 5.5; *B* 221.8, 38.2, 6.2, 22.9; *C* 159.1, 27.4, 11.8, 43.7; *D* 38.6, 6.6, 6.5, 23.9; *E* none; *F* 2.4, 0.4, 1.1, 4.1. Shrub taxa comprising 90% of the total number of shrubs: *Rhamnus catharticus,* 52.1, 100; *Cornus* spp., 15.5, 100; *Corylus* sp., 10.6, 90; *Ribes* spp., 9.42, 80; *Prunus* spp., 3.3, 90. Ground cover, 62%; canopy cover, 82%; mean canopy height, 14.5 m (range 11.3–15.2 m).

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COLOR AND SIZE VARIATION IN EASTERN WHITE-BREASTED NUTHATCHES

D. Scott Wood[1]

Abstract.—An analysis of 928 specimens of White-breasted Nuthatch (*Sitta carolinensis*) collected in eastern North America demonstrates that all nuthatches can be sexed in the hand, but determination of sex at a distance is subject to considerable error, especially in southeastern populations. All but three of the specimens examined can be sexed accurately using presence or absence of gray on the crown. At least 10% of the females in any population in eastern North America will appear to have dark crowns when viewed from a distance in the field; populations in the southeasternmost United States have a high frequency of females with dark crowns—83% in peninsular Florida and 40% in coastal plain populations in Alabama, Georgia, South Carolina, and northern Florida. Wing and bill lengths show a clinal geographic pattern, with the largest birds in the north and the smallest in Florida. Although peninsular Florida populations are the most distinct of any geographic area, I can find no criteria to identify more than 60% of them unequivocally in the absence of collecting locality data. For this reason I recommend that all White-breasted Nuthatches east of the Great Plains be considered one subspecies: *Sitta carolinensis carolinensis* Latham. *Received 25 Jan. 1992, accepted 24 April 1992.*

White-breasted Nuthatches (*Sitta carolinensis*) have been described as sexually dimorphic in plumage at least since Wilson (1808) who noted that the black of the crown of females is "less deep" than that of males. Dwight (1900) was more emphatic about the gray cap of females (at least of northern populations) stating that "females never, even in later plumages [after first winter], acquire enough black on the cap to be mistaken for males." Scott (1890) was apparently the first to notice that some female White-breasted Nuthatches have black crowns, when he used the presence of this feature to help characterize the peninsular Florida populations as a distinct subspecies (*S. c. atkinsi*). He noted that the crowns of some Florida females were partly suffused with gray.

Oberholser (1917) performed the first critical analysis of the species over its entire range in the eastern United States and concluded that Florida birds were indistinguishable from those in South Carolina, but that two forms were recognizable. He characterized *S. c. carolinensis* as occurring throughout the southeastern United States north to North Carolina, Kentucky, southern Indiana, and southern Illinois, and west to eastern Texas, and described a new subspecies *S. c. cookei* as occurring to the north of *carolinensis*. He restricted the type locality of the species to the mouth of the Savannah River in South Carolina. According to his

[1] Section of Birds, Carnegie Museum of Natural History, 4400 Forbes Ave., Pittsburgh, Pennsylvania 15213 (Present address: 1466 Shady Ave., Pittsburgh, Pennsylvania 15217).

analysis (p. 185), *S. c. cookei* differs from *carolinensis* by being "larger; upper parts lighter; lower parts more purely white; bill usually relatively less slender; and female with black of head usually overlaid with plumbeous."

Aldrich (1944) apparently considered crown color to be unimportant taxonomically since he failed to mention it in his revision of the species. He followed Oberholser but placed the zone of intergradation between *cookei* and *carolinensis* in North Carolina through Tennessee and southern Missouri. Mengel (1965) reviewed the differences between the eastern subspecies and concluded that the major difference between the two was in the proportion of black-crowned females, which was considerably higher in *carolinensis.* Greenway (1967) lumped all eastern populations into *carolinensis,* asserting that the northern populations are "distinguished only by the single character of a slightly paler back" (p. 139).

In their aging and sexing guide (United States Fish and Wildlife Service and Canadian Wildlife Service 1991) the Bird Banding Laboratory asserted that in White-breasted Nuthatches the sex of birds with black caps cannot be determined (reliably) in populations south of New Jersey, Pennsylvania and the Ohio River. My own experience with this species, both under banding conditions and in museum collections has suggested that this assertion may be overly cautious, and further search of the literature showed that the patterns of variability in female crown color were not well understood.

Apart from crown color, there seem to be few differences between sexes of White-breasted Nuthatches, and none that discriminates a majority of individuals. Mengel (1965) asserted that mean wing length differed between sexes but no statistical tests were made. The ranges reported in Pyle et al. (1987) also suggest that females have slightly shorter wings but this character was not rigorously examined by them. Both wing and bill lengths have been reported to show geographic variation (e.g., Oberholser 1917, Aldrich 1944) but no statistical analyses have been published.

No discussion of possible mis-sexing of museum specimens occurs in any of the reports cited above. Such specimens, if unrecognized, can lead to significant errors in analyses. For example, the number of female nuthatches with black crowns may be much inflated. Considerable personal experience with museum collections has demonstrated that, for species with even moderate sexual dimorphism in plumage, as many as 5% of the specimens in a collection are likely to have been mis-sexed. Parkes (1989) provides an extensive discussion on the prevalence of mis-sexed museum specimens.

In this study I have assessed the differences in external characteristics between male and female White-breasted Nuthatches east of the Great

TABLE 1
SPECIMENS OF WHITE-BREASTED NUTHATCH USED IN THIS STUDY

	Area[a]	Total males	Total females	Dark-crowned females (%)
1	Northeast	182	157	9.6
2	North central	50	37	10.8
3	Southern Appalachians	55	35	31.4
4	South central	40	22	22.7
5	Southeast	54	30	10.0
6	Florida and Georgia	71	43	62.8
7	Western edge	97	56	12.5
	Total	549	380	18.9
Alabama, Georgia, Florida, South Carolina samples				
A	Peninsular Florida	22	17	82.3
B	Coastal Plain	47	28	39.3
C	Piedmont	11	8	37.5

[a] See Fig. 1 for limits of geographic areas.

Plains. The following specific questions are addressed: (1) Can mis-sexed museum specimens be recognized? (2) What are the patterns of variation in crown color with respect to age, sex, and geography; are any differences significant? (3) Do significant differences in bill length or wing length exist between ages, sexes, or populations? (4) For which populations can live birds be reliably sexed in the hand? (5) For which populations can birds be reliably sexed at a distance in the field? and (6) What are the taxonomic implications?

MATERIALS AND METHODS

I measured 928 specimens of White-breasted Nuthatches collected east of the Great Plains (Table 1), from museum collections in the eastern United States and Canada (see acknowledgments for list). For each specimen, the following data were taken: location, date, sex, age, wing length (unflattened chord to the nearest 0.5 mm), bill length (from the distal margin of the nares to the tip of the upper mandible, to the nearest 0.1 mm), and crown color. For crown color, I divided the forehead, crown, and nape into five regions. Using the terminology of Pettingill (1985) these are: (1) anterior half of forehead; (2) posterior half of forehead; (3) crown except occiput; (4) occiput; and (5) nape. For each region I scored the color as: 0 = black; 0.5 = trace of gray (a few feathers); 1 = presence of gray but area appears dark; 2 = considerably gray (most feathers have gray tips). Other data were taken from the specimen labels.

White-breasted Nuthatches are considered non-migratory by most authors. Scattered anecdotal evidence of movements of individuals has been reported, especially for the fall season (e.g., Griscom and Snyder 1955, Mengel 1965), but there is no evidence of long-distance movements by members of this species; southern populations are not diluted by northern migrants during the winter. In this study I assumed that each specimen represented

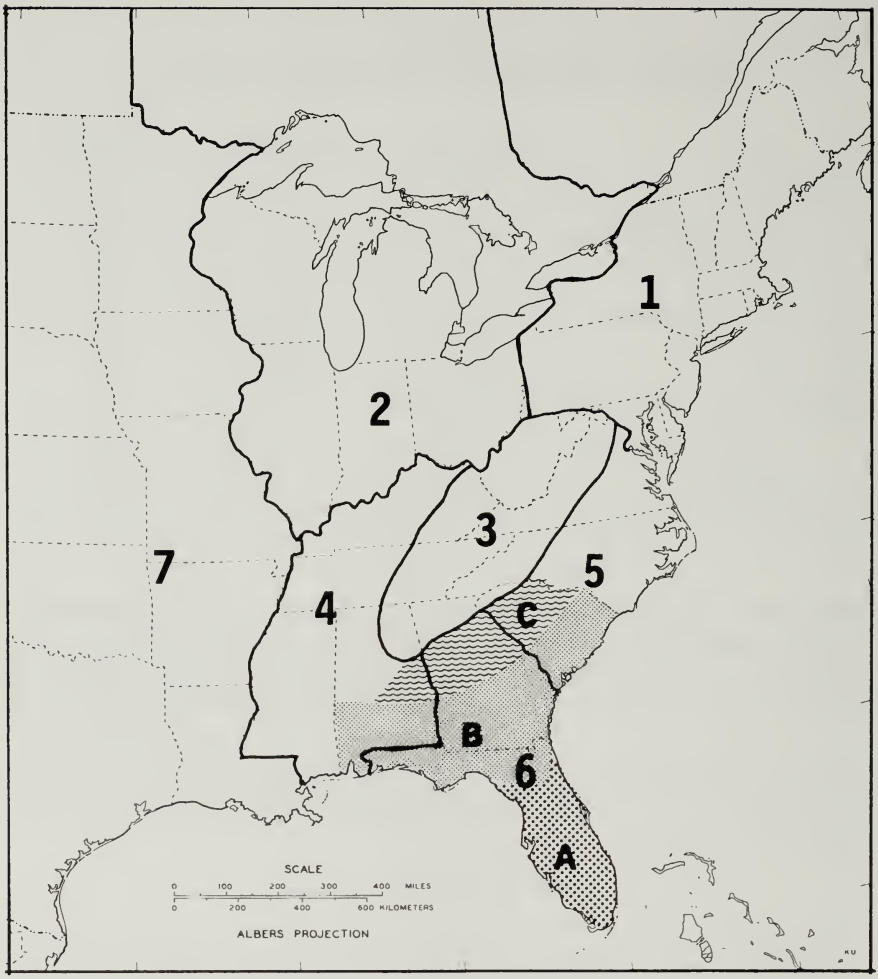

FIG. 1. Geographic regions used in this study. Outlined and numbered regions are the primary divisions; shaded and lettered regions are for the subsequent finer analyses.

the resident populations of the collecting locality, regardless of the date of collection. Each specimen was allocated to one of seven geographic regions (Table 1, Fig. 1). These were chosen (1) to reflect the conclusions of previous workers as indicated by the ranges of the subspecies each recognized and (2) to be sure that variation between broad ecogeographic units (such as between populations in the southern Appalachians and the adjacent piedmont) was not overlooked. Because the analysis using the original seven regions did not permit unequivocal taxonomic conclusions, I further divided the specimens from Alabama, Florida, Georgia, and South Carolina into three sub-regions corresponding to broad physiographic

areas recognized by Wayne (1910), Howell (1932), Burleigh (1958), and Imhof (1976); peninsular Florida; coastal plain north of peninsular Florida; and piedmont (Table 1, Fig. 1).

To assess the occurrence of mis-sexed museum specimens, I used a series of 40 carefully sexed recent specimens in the Carnegie Museum collections to evaluate plumage characteristics other than crown color that might provide suitable discrimination. I also compared ranges for wing and bill lengths of specimens of unequivocal sex to evaluate their discriminatory utility.

Few museum specimens bore any indication of age on the label, and no aging criteria are available that would apply to study skins (Pyle et al. 1987). To assess the effects of differences in wing length due to age, I used data from 208 birds (mostly in fresh fall plumage) banded at Powdermill Nature Reserve (the field station of Carnegie Museum of Natural History, located in Westmoreland County, Pennsylvania) for which sex (determined by crown color; equivocal individuals not included) and the plumage of the remiges were known. This sample was evenly divided between males and females and birds with first basic remiges and those with second or later basic remiges. An examination of the data from museum specimens used in this study showed that very young birds had much shorter bills than adults but that the adult length was attained within a few months of hatching. To reduce the age bias as much as possible in the analysis of bill length variation, I eliminated specimens with bill lengths shorter than the minimum for specimens taken between November and March (i.e., shorter than 11.0 mm for females and 11.8 mm for males), and I also eliminated any specimens taken during the period May through August that were marked as immature on the label.

The crown color of birds marked as immature or juvenile, especially those with rectrices still partly sheathed or those with very short bills, was examined to assess the variation in this character due to age. The juvenile plumage (especially the crown) appears to be replaced very soon after fledging and is very similar to postjuvenal plumages, except that any black on the crown is dull rather than shiny. In color, first basic plumage is essentially identical to later plumages; White-breasted Nuthatches do not have an alternate plumage. In analysis of crown color, all ages were pooled. I used the mean of the five crown scores to characterize overall crown color for each specimen. The distribution of gray on the crowns of females is not random; in all but a few instances, birds with reduced amounts of gray have the least on segments 3–5, and the most on segment 1. This permitted the following simple criterion for birds that would appear to have dark crowns when viewed at a distance (field criterion): any specimen with a score of less than 2 on crown segment 2 was noted as dark-crowned.

Analysis of numerical data was done using the BIOM statistical package (Rohlf 1989). Patterns of variation between sexes and geographic regions were evaluated using analysis of variance and the *GT2* method of pairwise multiple comparisons (Sokal and Rohlf 1981; programs BASTAT, NESTAN, MCPAIR, and RXC of BIOM). The comparison of frequency of black-capped females between peninsular Florida and the coastal plain areas was done using a contingency table and chi-square.

RESULTS

Identification of mis-sexed individuals.—Mensural characters are not useful for discriminating the sexes of White-breasted Nuthatches (see results below). However, Robert C. Leberman and Robert S. Mulvihill, banders at Powdermill Nature Reserve, suggested that the color of the outer margins of the secondaries and greater secondary coverts might discriminate the sexes. Careful examination of the reference series in

strong daylight confirmed this. On the closed wing, the outer edges of the secondaries produce a band of blue-gray color dorsal to the mostly dark edges of the primaries. In males the blue-gray of these secondary edges shows no hint of brownish or greenish wash, whereas in females the blue-gray is duller and with a greenish or brownish cast (when compared directly to a typical male). This distinction often applies to the back feathers as well, although it is more difficult to assess. Examination of the crown color of the birds in the reference series showed that males invariably had shiny black crowns with no trace of gray on the tips of any feathers (some birds had a few *white* feathers mixed in with the black near the base of the bill, but these were quite different from the gray-tipped feathers typical of females). Females, on the other hand, always had gray tips to at least some crown feathers. In the reference sample, most showed a nearly solid gray cap (nearly all feathers had gray tips), but a few birds had so little gray as to appear black from any distance.

Applying the wing color criterion to a much larger sample, including all specimens for which crown color and label information appeared to disagree (specimens marked as male but with gray in the crowns; specimens marked as female but with dark crowns) revealed that, with three exceptions, all specimens with female-type wings also had at least a few gray feathers in the crown, and all specimens with male-type wings had solid shiny black crowns. The remaining three specimens (all from U.S. National Museum: 195759, Washington, D.C., 15 May 1888; 352989, Middleboro, Kentucky, 20 September 1938; 524553, Washington, D.C., 6 February 1899) are labeled as females and have female-type wings but have no traces of gray in the crowns. These birds I treated as females in subsequent analyses. Of the 928 specimens I examined, I believe 38 were incorrectly sexed; 11 males that were recorded as females, and 27 females that were recorded as males. Many of the latter had solid gray crowns; apparently earlier workers assumed these birds were mis-sexed since there is no mention in their reports of males with gray crowns.

Patterns of variation between sexes and among geographic regions.— Males always have entirely shiny black crowns, regardless of population; there is no geographic variation in this character. Significant variation exists among geographic areas for overall female crown color (Table 2; $F = 12.90$, $df = 7,334$, $P < 0.001$). However, this is entirely accounted for by Region 6 (Florida and Georgia) which differs significantly from all others ($GT2 \geq 3.253$, $P < 0.01$). No other significant differences were detected between geographic areas. Females from Region 6 have, on average, much darker crowns than birds in other parts of the eastern United States. Table 1 lists the percentage of dark-crowned females (field criterion rather than mean crown score) recorded for each geographic region.

TABLE 2

BASIC STATISTICS FOR WING AND BILL LENGTHS AND CROWN COLOR BY SEX AND GEOGRAPHIC AREA

Region	Males		Females	
	N	Mean (± SE)	N	Mean (± SE)
Wing				
1	164	89.6 (±0.15)	132	88.6 (±0.16)
2	48	89.3 (±0.30)	28	88.4 (±0.46)
3	49	89.0 (±0.23)	29	86.8 (±0.31)
4	35	88.0 (±0.33)	19	85.8 (±0.44)
5	51	88.2 (±0.29)	26	86.7 (±0.49)
6	63	86.9 (±0.27)	39	85.3 (±0.39)
7	91	88.6 (±0.28)	48	87.1 (±0.35)
Bill				
1	153	14.34 (±0.92)	120	13.13 (±0.56)
2	45	13.38 (±0.92)	29	13.07 (±0.12)
3	46	13.45 (±0.72)	24	12.81 (±0.92)
4	34	13.10 (±0.90)	19	12.45 (±0.16)
5	51	13.17 (±0.83)	27	12.48 (±0.20)
6	61	13.24 (±0.73)	36	12.59 (±0.95)
7	84	13.44 (±0.63)	44	12.86 (±0.86)
Crown color				
1			134	1.81 (±0.40)
2			30	1.76 (±0.76)
3			29	1.56 (±0.95)
4			19	1.49 (±0.15)
5			27	1.75 (±0.81)
6			39	1.06 (±0.85)
7			48	1.79 (±0.59)
A			17	0.68 (±0.83)
B			28	1.05 (±0.92)
C			8	1.02 (±0.21)

No significant differences in bill length were found between sexes ($F = 3.64$, df = 1,13, $P > 0.05$), but significant variation was demonstrated among geographic areas ($F = 11.56$, df = 13,737, $P < 0.001$). For comparisons between areas, data for both sexes were pooled; basic statistics are shown in Table 2. Seven comparisons were found to show significant differences: Region 4 versus Regions 1, 2, 3, and 7 (smallest $GT2 \geq 3.15$, $P < 0.05$); Region 5 versus Regions 1 and 7 ($GT2 = 3.05$, $P < 0.05$); and Region 6 versus Region 1 ($GT2 = 5.33$, $P < 0.01$). Bill length averages larger in the north and smaller in the south. Populations in the southern

Appalachians are more like those to the north than they are to other populations of similar latitude.

Mean wing lengths for the Powdermill Nature Reserve banding sample were: immature female 88.173 (SD = 2.303, N = 52); immature male, 90.040 (SD = 4.723, N = 50); adult female, 90.367 (SD = 3.341, N = 49); adult male, 91.316 (SD = 3.488, N = 57). Analysis of variance demonstrates that most of the variation is attributable to age (between sexes $F = 1.38$, $P > 0.5$; between ages $F = 23.86$, $P < 0.01$). Immature females are significantly smaller than any other age and sex class (versus adult female, $GT2 = 5.93$, $P < 0.01$; versus immature male, $GT2 = 5.07$, $P < 0.01$), and immature males are significantly smaller than adult males ($GT2 = 5.93$, $P < 0.01$; versus immature male, $GT2 = 5.07$, $P < 0.01$), and immature males are significantly smaller than adult males ($GT2 = 3.54$, $P < 0.01$). In the sample taken from museum specimens, I was not able to separate first year birds from those older than one year. The Powdermill data suggest that, with ages pooled, differences detected between sexes might be actually due to age because the inclusion of immature females should lower the mean for females more than the inclusion of immature males would lower the mean for males. This turned out not to be a problem because the specimen data failed to show significant variation between sexes ($F = 2.83$, df = 1,14, $P > 0.05$); the sexes were pooled in subsequent analyses. Significant variation was found among geographic areas ($F = 14.26$, df = 14,835, $P < 0.01$). In geographic comparisons, Region 6 (with the smallest mean) was significantly different from all others except Region 4 (vs Region 5, $GT2 = 4.148$, $P < 0.01$). Region 1 (with the largest mean) was significantly different from all others except Region 2 (vs Region 3, $GT2 = 3.37$, $P < 0.05$). In addition, Region 2 was significantly different from Regions 4 and 5 (vs Region 5, $GT2 = 3.49$, $P < 0.05$). No other comparisons were significant.

Variation between populations in the southeastern United States.—No significant difference was detected in bill length between any of the three physiographic regions A, B, and C, or for any character between the piedmont and the coastal plain. Wing length, however, differed significantly ($F = 9.76$, df = 1,113, $P < 0.01$) between peninsular Florida and the coastal plain populations. While mean crown color did not differ significantly between peninsular Florida and coastal plain populations, a contingency table testing the independence of geography (peninsular Florida vs coastal plain) and crown color (using the field criterion) demonstrated that these were not independent (peninsular Florida, 14 dark-crowned, 3 gray-crowned; coastal plain, 11 dark-crowned, 17 gray-crowned; G-statistic > 7.3, $P < 0.01$). Table 1 lists the percentage of dark-crowned females in each of the three physiographic subregions of the southeastern

United States. Populations in peninsular Florida show a frequency of 82%, nearly twice that of the adjacent coastal plain or piedmont populations. Peninsular Florida birds average smaller in wing length and have a higher percentage of females with dark crowns than coastal plain populations in Alabama, Georgia, and South Carolina.

DISCUSSION

Use of museum collections.—Museum collections are exceedingly important resources for answering many kinds of biological questions (and may be the only source of data pertinent to some questions). One unfortunate reality is that errors exist in the data associated with these specimens. A fundamental part of any study involving museum collections must be the assessment of such errors. In the present study, if the label data regarding sex were used uncritically, the conclusions would have been quite different (e.g., an assertion that males could have gray crowns). Considerable experience suggests that for sex information, an error rate of 5% is not unexpected. The error rate detected in this study is just over 4%, for a species in which sexual dimorphism in plumage is not glaringly obvious.

Variation due to age and sex.—With the exception of sex differences in crown and wing color, White-breasted Nuthatches show little variation between age and sex classes. The mean wing length for birds in first basic plumage is shorter than for birds in later plumages, but the ranges overlap to a great extent. Immature females tend to have especially short wings. The bills of juvenile birds do not reach adult length for several months after fledging, but otherwise there are no differences between age and sex classes for this character. Juvenal plumage is duller (especially the crowns of males) than first basic plumage, but first basic plumage, which is attained rather quickly after fledging, is essentially identical to subsequent plumages. Crown color and the color of the outer margins of the secondaries are sexually dimorphic.

Geographic variation.—Variation in bill and wing lengths in White-breasted Nuthatches appears to be clinal in the eastern United States; populations with the largest means for these characters are in the Northeast, whereas the smallest are in the southern states. Populations in the southern Appalachians are intermediate but larger than those in other areas at the same latitude. Crown color of females shows the strongest geographic patterning: the average crown color of females in Florida and Georgia (south of the Appalachians) is significantly darker than in any other population; other populations show no significant differences in this character. The frequency of females with crowns that would appear black at a distance is significantly higher in peninsular Florida than for popu-

lations on the southeastern coastal plain, and is higher for populations in the southern United States (including those in the Appalachians) than in the north.

Determining the sex of live birds.—In the hand, the sex of virtually all White-breasted Nuthatches can be determined correctly using the criterion of crown color (3 of 928 would have been mis-sexed in this sample): if any crown feathers have gray tips, the bird is a female; if the crown is solid shiny black and no feathers have gray tips, the bird is a male. Males may have a few white feathers mixed in with the black near the base of the upper mandible, but these feathers are all white, not dark with gray tips. In females with dark crowns, the feathers with gray tips are usually on the forehead, but are on the nape in a few individuals. It should be emphasized that even in the hand some females have so little gray as to be easily overlooked, especially in poor light. However, such females occur at very low frequencies (less than 1–2%) in all populations, even those in Florida and Georgia. The color of the edges of the secondaries can be used to corroborate the conclusions drawn from crown color, but this criterion is difficult to apply without a reference (e.g., an adult male study skin in fresh plumage).

Determining the sex of birds in the field at a distance is considerably more difficult. East of the Great Plains, at least 10% of all females regardless of population have little enough gray in the crown to be easily mistaken for males (Table 1). During the breeding season, when the birds are paired, careful observation should be able to separate the sexes in most cases. However, after the young have fledged and the birds are in family groups, determining the sex of individuals with dark crowns will be subject to an error rate approaching 10%. In Florida and Georgia south of the Appalachians, the field situation is far worse: 40%–80% of the females appear to have dark crowns. I suspect that the only way to keep the error frequency low when working with these populations is to use color markers.

Taxonomic implications.—Oberholser (1917) suggested that the colors of the back, underparts, and (in females) crown differed between northern (i.e., New England) and southern (i.e., Florida) White-breasted Nuthatches. He also thought southern birds were smaller than northern ones. Aldrich (1944) restricted the principal distinction between Oberholser's races (*Sitta carolinensis carolinensis,* and *S. c. cookei*) to back color, *S. c. cookei* was considerably lighter in color. Mengel (1965) carefully reassessed these characters as they applied to Kentucky birds (where the two races supposedly intergraded) and concluded that, while it was possible that average color differences existed, such characters were of little use in

assigning specimens to one or the other race. He thought the principal difference between the races was the frequency of dark-crowned females in the populations: such birds were common in populations of *S. c. carolinensis,* and rare in populations of *S. c. cookei.* Like Mengel, I am not able to appreciate the difference in back or underpart colors between southern and northern birds; the range of variation in these characters appears to my eye to be very similar in most populations. Mensural characters, being clinal for this species, also do not distinguish sets of populations at a subspecific level. Female crown color, however, shows a more distinct geographic pattern. Populations in the southeastern United States (especially Georgia and Florida) show a much higher frequency of dark-crowned females. Finer analysis shows that the populations in peninsular Florida account for much of this difference. Although Mengel (1965) considered all populations south of the Ohio River to show a similar frequency of black-crowned females, my analysis indicates otherwise. At least one of the black-crowned females used in Mengel's analysis was, I believe, mis-sexed, and others have varying amounts of gray in the crowns (I was not able to reassemble all of his material). While the populations of my Region 4 (which includes the part of Kentucky with Mengel's southern birds) show a higher frequency of dark-crowned females than areas to the north, the average crown color is not significantly different.

My data suggest that like a number of other species (Howell 1932), populations of White-breasted Nuthatch in peninsular Florida have followed a somewhat different evolutionary history from those in other areas. Peninsular Florida birds have significantly shorter wings than those to the north, and the frequency of females with dark crowns (83%) is nearly twice that of any other region. Populations on the coastal plain to the north of peninsular Florida are most similar to the Florida birds; they average smaller than birds from farther north and have a higher percentage of dark-crowned females than more northern populations. I do not, however, recommend that two subspecies be formally recognized east of the Great Plains. Such recognition implies that individuals can be assigned relatively unambiguously to one or the other taxon in the absence of data on geographic origin. I am unable to provide criteria that would correctly assign more than 60% of the specimens in my sample.

It is possible that historic changes have taken place in some of these nuthatch populations; the species is believed to be close to extinction in peninsular Florida (Stevenson 1978). Many of the specimens in the relatively small sample from the southeastern United States are from nearly a century ago and may not accurately represent the morphology found in

current populations. Much more collecting and field study of this species is needed in Alabama, Georgia, Florida, and South Carolina to clarify the present patterns of morphological characteristics.

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GEOGRAPHIC VARIATION IN SIZE OF THE EASTERN KINGBIRD

NICOLE R. VAN WYNSBERGHE,[1] JAMES D. RISING,[1] AND DAVID I. MACKENZIE[2]

ABSTRACT.—We analyzed geographic variation in 12 (female) and 14 (male) morphometric characters of 428 (264 male and 164 female) Eastern Kingbirds (*Tyrannus tyrannus*) from North America. There is significant sexual dimorphism in the Eastern Kingbird: males have longer tails, wing-tips, and bills than females. This perhaps reflects the aerial courtship displays and aggressive territorial defense performed principally by males. There appears to be little difference in size between the sexes. There is no geographic variation in the degree of sexual dimorphism, indicating either that the extent of dimorphism is not influenced by interspecific competition (as predicted by the niche variation hypothesis) or that such competition is not significant for *T. tyrannus*. Although there is significant geographic variation in both sexes for all variables measured, the amount of this variation is slight and not clearly ordered in a geographic pattern. Eastern Kingbirds, for example, do not seem to show variation that conforms to Bergmann's Rule. In both sexes, there is a northwest-to-east trend of decreasing size for most characters measured, but a posteriori tests delimit few, and broadly overlapping, statistically homogeneous sets. There is no indication of character displacement in size in populations where *T. tyrannus* is sympatric with congeners even though their ecology and habits are similar. *Received 3 Sept. 1991, accepted 25 April 1992.*

The Eastern Kingbird (*Tyrannus tyrannus*) breeds from north-central British Columbia, northwest Saskatchewan, central Manitoba, central Ontario, southern Quebec, Prince Edward Island, and Nova Scotia south to northeastern California, northern Nevada, northern Utah, northeastern New Mexico, the Gulf coast of the United States, and southern Florida (A.O.U. 1983, Fig. 1). The species is migratory and winters in South America. Although the Eastern Kingbird is widespread and one of the commonest North American breeding birds, there has been no comprehensive study of geographic variation of the species (Zink and Remsen 1986). Here we describe patterns of geographic variation in size and sexual dimorphism on the basis of measurements of specimens taken from virtually throughout the species' range, and test hypotheses about the evolution of geographic variation.

MATERIALS AND METHODS

Populations.—We measured 428 specimens (see Acknowledgments) collected between May and August, when the birds are breeding, and thus all probably breeding individuals. At that time of year, all individuals are to some extent worn, but we omitted from analyses birds that were judged to be damaged excessively. We examined (264 males, 164 females)

[1] Dept. of Zoology, Univ. Toronto, Toronto, Ontario Canada M5S 1A1.
[2] Deceased.

FIG. 1. The distribution of Eastern Kingbirds (*Tyrannus tyrannus*).

specimens from most parts of the species' range; unfortunately Florida was excluded because of small sample size. We analyzed sexes separately, and initially sorted both sexes into 10 geographic populations, from regions of approximately equal size (5° latitude and 10° longitude), each containing at least 17 males and 10 females (Fig. 2). These samples were used to quantify sexual dimorphism. After finding significant size dimorphism, we sorted specimens into 18 populations of males and 10 populations of females for analyses of geographic variation (Tables 1 and 2). These samples are of somewhat unequal geographic size, but each contains approximately the same number of individuals. This enabled us to increase the extent of geographic coverage. We identify regions by the name of a province or state prominently included in the samples.

Characters.—Following Baldwin et al. (1931), MacKenzie measured the following 12 features on each study skin with dial calipers to the nearest 1.0 mm for feathers, and to the nearest 0.1 mm for bill and tarsus: *wing length* (*WL*), the cord of the unflattened, closed wing from the farthest anterior point on the anterior edge of the wrist joint to the tip of the longest primary feather; *wing-tip to 10th* (*T10*), *wing-tip to 5th* (*T5*), *wing-tip to 4th* (*T4*), and

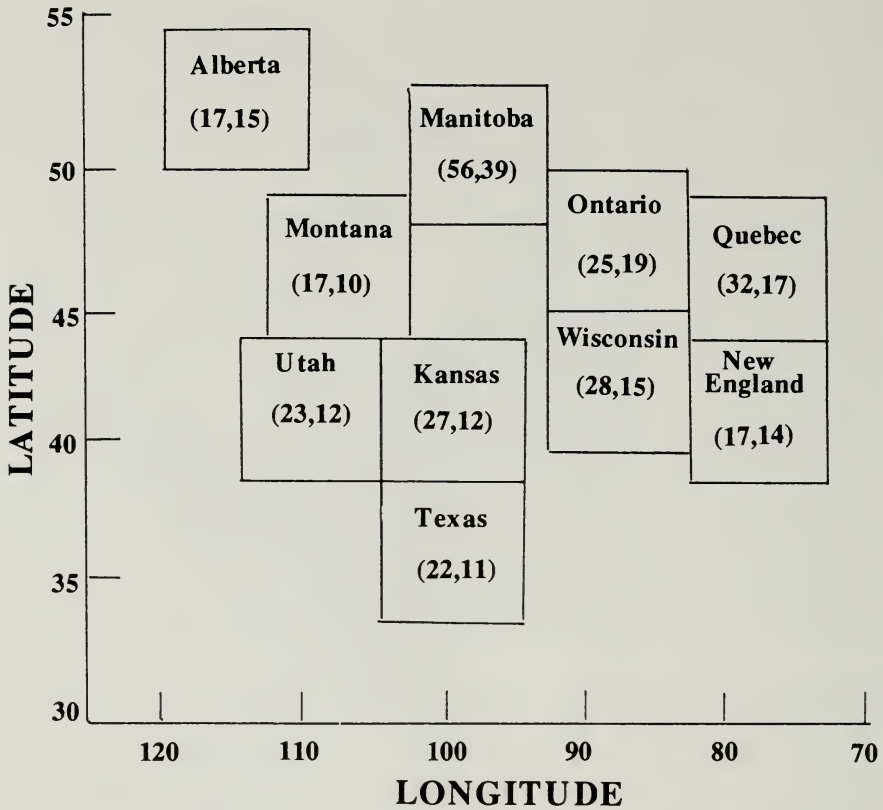

FIG. 2. Geographical positions of the samples used to determine patterns of sexual dimorphism in Eastern Kingbirds. Numbers of males and females are in parentheses. Each sample includes areas outside the area of the sample name. For example, the sample named Utah includes birds from parts of Idaho, Utah, Wyoming, and Colorado, and the sample named Texas includes birds from parts of Colorado, New Mexico, Kansas, Oklahoma, and Texas.

wing-tip to secondary (*TSC*), the distance on the closed wing from the tip of the longest primary to the tip of the 10th, 5th and 4th primary feathers, and to the longest secondary feather; *outer tail length* (*OTL*) and *inner tail length* (*ITL*), the distance from a point between the insertions of the two middle rectrices to the tip of the longest outer and longest inner tail feathers; *tarsus length* (*TRL*), the diagonal distance from the middle posterior point of the joint between the tibiotarsus and tarsometatarsus, to the lower anterior edge of the lowest undivided scute of the junction of the tarsometatarsus with the base of the middle toe; *total culmen length* (*CLL*), the chord of the bill from the point where the integument of the forehead meets the horny covering of the bill to the tip of the culmen; *culmen length* (*from nares*) (*CLN*), the chord of the bill from the anterior margin of the nares to the tip of the culmen; *culmen width* (*CLW*), the distance between the two cutting edges of the bill, at the anterior end of the nares; and *culmen depth* (*CLD*), from the upper edge of the culmen to

TABLE 1
SAMPLES OF FEMALE EASTERN KINGBIRDS: NAMES AND COORDINATES

Sample location	Latitude (°N)	Longitude (°W)
British Columbia (BC)	47–57	113–122
Saskatchewan (SK)	46–54	104–112
Manitoba (MB)	46–54	95–101
Northern Ontario (NO)	46–55	79–88
Southern Ontario (SO)	43–45	80–86
Pennsylvania (PA)	37–45	72–79
Utah (UT)	36–45	104–114
Kansas (KS)	36–43	99–103
Missouri (MO)	34–40	92–95
Kentucky (KY)	34–42	80–89

the lower edge of the mandible, at the anterior end of the nares. In adult kingbirds the inner webs of the longest primaries are cut out, especially in breeding males (Pyle et al. 1987). Therefore, on males, we also measured the *length* and *width of the tip of the longest primary* (*PML PMW*); thus, for males we examined 14 characters.

For the interspecific comparisons required to test our prediction about the relative size

TABLE 2
SAMPLES OF MALE EASTERN KINGBIRDS: NAMES AND COORDINATES

Sample location	Latitude (°N)	Longitude (°W)
British Columbia (BC)	47–53	112–122
Alberta (AB)	49–54	106–114
North Dakota (ND)	47–52	99–104
Manitoba (MB)	48–53	92–98
Northern Ontario (NO)	47–55	80–90
Wyoming (WY)	44–46	103–113
Wisconsin (WI)	44–46	85–93
Southern Ontario (SO)	44–46	80–84
New England (NE)	44–47	70–79
Utah (UT)	40–43	110–112
Nebraska (NK)	40–43	99–106
Illinois (IL)	40–43	88–97
Ohio (OH)	40–43	80–86
Pennsylvania (PA)	40–43	72–79
New Mexico (NM)	36–39	103–106
Texas (TX)	35–39	99–102
Oklahoma (OK)	34–44	91–98
North Carolina (NC)	31–34	77–84

TABLE 3

MEAN MEASUREMENTS (MM) OF 12 VARIABLES FOR FEMALE EASTERN KINGBIRDS[a]

Sample (N)	WL	T10	T5	T4	TSC	OTL	ITL	TRL	CLL	CLN	CLW	CLD
BC (16)	115	6	22	27	27	80	84	18.8	22.1	13.4	7.6	6.2
SK (12)	114	5	22	27	28	81	84	19.3	22.1	13.6	7.8	6.3
MB (41)	114	7	22	28	27	81	83	19.0	22.2	13.6	8.0	6.4
NO (13)	112	6	22	27	25	78	81	18.8	21.2	13.1	7.7	6.5
SO (27)	112	6	21	27	25	79	82	18.7	21.4	13.2	7.7	6.4
PA (19)	112	6	21	27	28	80	82	18.6	21.9	13.3	7.7	6.2
UT (19)	114	6	22	27	29	80	83	19.1	21.8	13.3	7.7	6.2
KS (14)	112	6	21	26	29	80	83	18.9	21.7	13.3	7.6	6.3
MO (16)	112	6	21	26	28	78	81	18.9	22.1	13.5	7.7	6.1
KY (17)	112	6	22	26	25	79	82	18.8	21.4	13.2	7.8	6.3

[a] Sample names are identified in Table 1; variables are identified in the text.

of the species in sympatry and allopatry, we used measurements (also made by MacKenzie) on 561 Western Kingbirds (*T. verticalis*) and 234 Cassin's Kingbirds (*T. vociferans*) (comparable feather measurements on Scissor-tailed Flycatchers [*T. forficatus*] are not available). For this interspecific comparison we used only eight characters: wing length, outer and inner tail feather lengths, tarsus length, total culmen length, culmen length from nares, culmen width and culmen depth. Because skin measurements were not available for Scissor-tailed Flycatchers, Rising measured 27 features on 91 skeletons of males of four species of *Tyrannus*: 31 Cassin's Kingbirds, 25 Western Kingbirds, 21 Eastern Kingbirds, and 14 Scissor-tailed Flycatchers. The characters include those described by Rising (1988), as well as the length of the premaxilla from the skull, the phalanx length, and the length of the synsacrum. Not enough skeletal material for females was available to warrant analyses.

Statistical methods.—We calculated the means and standard deviations for each of the variables (Tables 3 and 4). Univariate evidence of geographic variation and sexual dimorphism among the 10 samples (Fig. 2) was tested with two-way ANOVAs (SAS 1987). One-way ANOVAs followed by a posteriori Student-Newman-Keuls (SNK) (SAS 1987) tests were used to elucidate patterns of geographic variation for each sex.

We used principal components analysis (PCA) (NTSYS/FACTOR, Version 4, Level 6, 1984; Rohlf 1985) on a matrix of correlations among the averages for the 12 characters of males and females from the 10 localities delimited in Table 1. Within sex, we used PCA on correlations of the sample means of the 18 males (14 characters) and 10 females (12 characters) samples to detect broad patterns of geographic variation. For interspecific comparisons, we again used PCA, based on matrices of correlations among means of Eastern, Western, and Cassin's kingbirds, with sexes analyzed separately. To assess evidence of character displacement, we divided the Eastern Kingbirds into three groups, those that are from allopatric populations ("allopatric," Fig. 4), and those that are from areas where they would be sympatric with Western Kingbirds ("sympatric-2"), and those that would be sympatric with both Western Kingbirds and Scissor-tailed Flycatchers ("sympatric-3"). For the skeletal data, we used all 91 (male) individuals, and did a PCA on the matrix of correlations among the 27 variables.

We used Mantel's test (1967) to compare matrices of phenotypic differences (average taxonomic distances based on averages of all 14 or 12 skin measurements) and matrices of

Table 4

Mean Measurements (mm) of 14 Variables for Male Eastern Kingbirds.[a]

Sample (N)	WL	T10	T5	T4	TSC	TPL	TPW	OTL	ITL	TRL	CLL	CLN	CLW	CLD
BC (17)	120	6	25	30	31	8.8	3.1	84.8	87.1	18.9	22.3	13.4	7.7	6.3
AB (19)	119	6	25	31	29	9.5	3.0	85.3	87.1	19.0	22.1	13.5	7.5	6.2
ND (17)	120	6	25	31	31	9.1	3.0	84	88	19.2	22.3	13.7	7.6	6.2
MB (49)	118	7	25	31	28	9.7	3.0	85.0	87.2	18.9	22.3	13.7	7.7	6.2
NO (10)	119	5	25	31	31	8.9	3.1	84.8	87.2	18.8	21.7	13.6	7.5	6.1
WY (11)	120	6	25	31	30	9.3	3.3	84	87	19.6	22.1	13.6	7.7	6.1
WI (19)	116	6	25	30	28	8.3	3.1	82	85	19.1	21.9	13.4	7.5	6.4
SO (20)	116	6	24	29	27	8.4	3.1	81.7	84.4	18.6	22.0	13.3	7.4	6.1
NE (21)	117	6	24	29	32	8.7	3.0	81	86	18.2	21.8	13.4	7.5	6.2
UT (14)	119	6	24	30	31	8.3	3.0	84	87	19.0	22.5	13.8	7.7	6.0
NK (13)	120	6	25	31	33	8.8	3.2	84	86	19.3	22.8	14.0	7.6	6.2
IL (16)	117	6	24	29	31	8.1	3.0	82	84	19.0	22.1	13.5	7.5	6.3
OH (19)	119	6	25	31	29	9.7	3.1	84	87	18.6	22.1	13.6	7.6	6.2
PA (10)	116	6	24	29	32	8.3	3.0	81.6	84.9	18.6	21.6	13.5	7.6	6.3
NM (12)	119	6	24	31	34	9.5	3.0	85	87	16.2	22.1	13.7	7.6	6.1
TX (17)	116	6	24	30	31	8.7	3.0	82	84	16.7	22.2	14.0	7.5	6.2
OK (13)	117	6	24	30	30	8.6	3.0	82	84	16.4	22.5	13.9	7.6	6.1
NC (11)	116	6	24	29	34	8.5	3.0	80	83	17.2	21.3	13.5	7.5	6.2

[a] Sample names are identified in Table 2; variables are identified in the text.

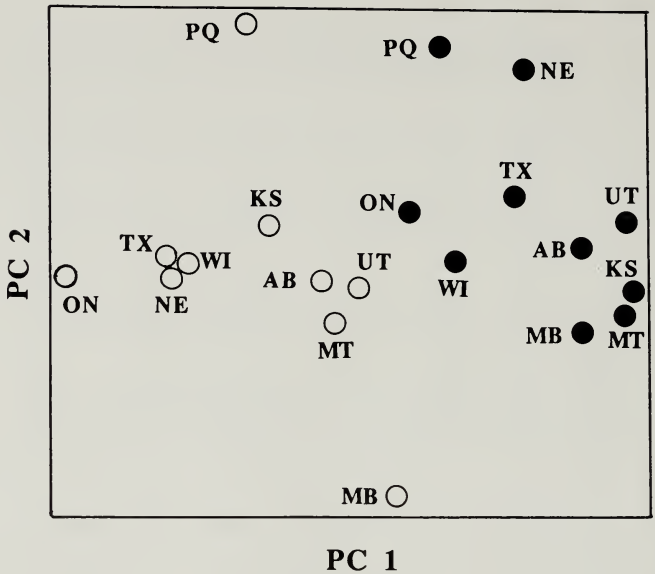

FIG. 3. Two-dimensional plot showing the positions of 10 samples of male (black dots) and female (open dots) Eastern Kingbirds in the space defined by principal component 1 and principal component 2 from a principal components analysis of the correlations among the averages of 12 measurements. The abbreviations used for the samples are: AB = Alberta, KS = Kansas, MB = Manitoba, MT = Montana, NE = New England, ON = Ontario, PQ = Québec, TX = Texas, UT = Utah, and WI = Wisconsin; these samples are all from areas of equal geographic size, and are the ones delimited in Fig. 2.

geographic distances and reciprocals of geographic distances. These tests indicate whether or not patterns of phenotypic variations simply reflect the geographic distances among the localities; the reciprocals emphasize patterns of variation among geographically close localities. NTSYS-PC, version 1.50, program MXCOMPG (Rohlf 1988) was used for Mantel's tests; 1000 random permutations were done for each test.

RESULTS

Sexual dimorphism.—Ten of 12 characters exhibited significant sexual dimorphism ($P < 0.05$ for bill height and $P < 0.001$ for the others) (Table 5). We found no sexual dimorphism in tarsus length or length of wingtip to the 10th primary, but we did find significant dimorphism in all measures of bill size. The interaction between sex and locality was not significant for any of the 12 features, indicating that there is no geographic variation in the magnitude of sexual dimorphism. In PCA among the 10 sample means for both sexes, the first component (PC 1) explains 48.0%, PC 2, 19.2%, and PC 3, 11.0%. The next several components are of nearly equal size, and each explains little of the total variance; thus, these are

TABLE 5

RESULTS OF TWO-WAY ANOVA OF GEOGRAPHICAL VARIATION AND SEXUAL DIMORPHISM AMONG EASTERN KINGBIRDS

Variable	Among samples (df = 9)	Between sexes (df = 1)	Interaction (df = 9)	Larger sex
Wing length	***	***	ns[a]	m > f
Tip to 10th length	**	ns	ns	m = f
Tip to 5th length	***	***	ns	m > f
Tip to 4th length	***	***	ns	m > f
Tip to secondary length	***	***	ns	m > f
Outer tail length	***	***	ns	m > f
Inner tail length	***	***	ns	m > f
Tarsus length	***	ns	ns	m = f
Total culmen length	***	***	ns	m > f
Culmen from nares	***	***	ns	m > f
Culmen width	***	***	ns	f > m
Culmen depth	***	*	ns	f > m

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; [a] ns = $P > 0.05$.

not discussed here. PC 1 is highly and positively correlated with measures of wing, and especially wing tip length, tail length, and bill length, and negatively correlated with bill height; PC 2 is negatively correlated with measures of bill size, and wing and tarsus length (Table 6). The PC 1 axis separates males from females (Fig. 3), with males having larger PC 1 scores, and hence longer tail feathers, wing-tips, and bills than females. Birds from the Québec sample and New England (especially males) have large values for PC 2, whereas those from Manitoba (especially females) have low values (Fig. 3).

Interspecific differences.—In the among-species PCAs for both males and females, the correlations of all eight variables are high and positive with the first component (Table 7), which represents an approximate measure of overall body size (Rising and Somers 1989). For both sexes, the three samples of Eastern Kingbirds cluster together, and are smaller on the PC 1 axis than the Western Kingbird which is, in turn, smaller than the Cassin's Kingbird (Fig. 4). Also in both sexes PC 2 is positively correlated with tail length and negatively correlated with tarsus and bill lengths (Table 7); thus populations with high values for PC 2 have relatively long legs and bills, and short tails. Western Kingbirds are separated from the others on this axis (Fig. 4). Thus, with regard to these eight study skin measurements, Eastern Kingbirds are smaller than either of the other two, but are similar in PC 2 values to Cassin's Kingbirds. In both sexes, however, the populations that are sympatric with Western Kingbirds

TABLE 6

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST THREE PRINCIPAL COMPONENTS FROM A PRINCIPAL COMPONENTS ANALYSIS OF A MATRIX OF CORRELATIONS AMONG THE AVERAGES OF 12 MEASUREMENTS FOR MALE AND FEMALE EASTERN KINGBIRDS

Character	PC 1	PC 2	PC 3
Wing length	0.41[a]	−0.53	0.34
Wing tip to 10th		−0.62	0.55
Wing tip to 5th	0.90		
Wing tip to 4th	0.91		
Wing tip to secondary	0.80		−0.30
Outer tail length	0.92		
Inner tail length	0.89		
Tarsus length	0.34	−0.67	−0.47
Total bill length	0.81	−0.34	−0.35
Culmen length (from nares)	0.79		−0.43
Culmen width (at nares)		−0.81	
Culmen depth (at nares)	−0.48	−0.54	
Eigenvalue	5.8	2.3	1.3
Variance explained	48.0%	19.2%	11.0%

[a] Correlations <0.30 not printed.

("sympatric-2" in Fig. 4) are also the ones that are most like Western Kingbirds on the PC 1 axis, and the differences among the three groups of Eastern Kingbirds on the PC 2 axis seem inconsequential. Thus, we see no evidence for character displacement in these data.

In the PCA of the 27 skeletal variables, of 91 individuals of four species of *Tyrannus,* the first PC explains 45.7% of the total variance, the second 10.8%, and the third 7.4% (Table 8). All of the variables are positively correlated with PC 1, and all of the correlations are greater than 0.4; thus the PC 1 scores are an approximate measure of overall body size (Rising and Somers 1989). PC 2 contrasts measures of bill size with measures of pectoral girdle size (scapula, sternum, etc.) and synsacrum size; thus, individuals with large PC 2 scores have relatively small bills and large pectoral girdles (Table 8). In the plot (Fig. 5) of PC 1 vs PC 2, Eastern Kingbirds and Scissor-tailed Flycatchers overlap considerably on the PC 1 axis (and thus are of similar body size); there is also substantial overlap of these two species with the Western Kingbird; Cassin's Kingbird generally tends to be of larger body size.

On the PC 2 axis there is again considerable overlap among species, especially among Eastern and Western kingbirds and Scissor-tailed Flycatchers. Thus these three *Tyrannus* are very similar in skeletal size, although the Eastern Kingbird tends to be smaller than the others (small PC 1 values) with relatively larger bill and pectoral elements (large PC 2

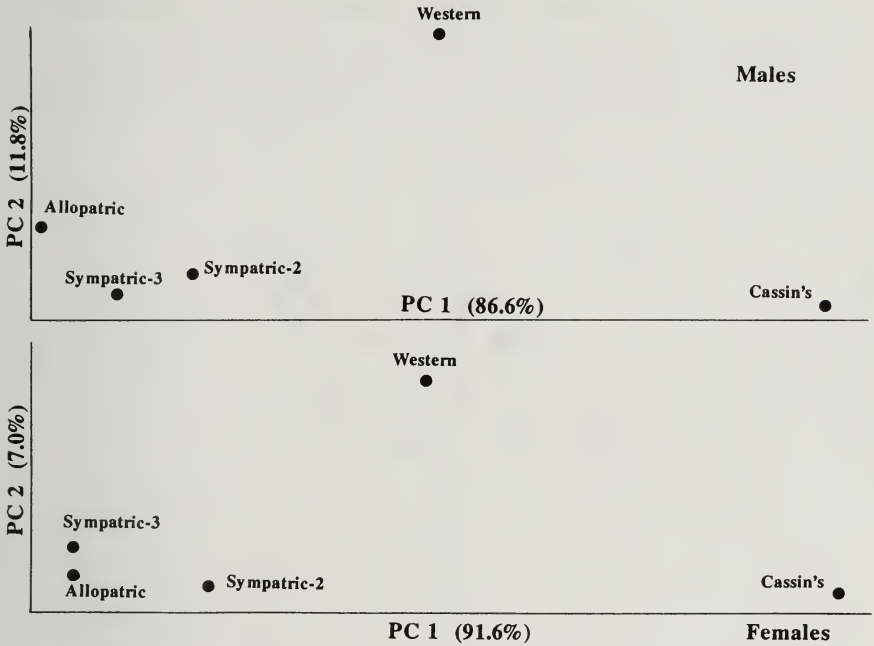

FIG. 4. Two-dimensional plots of the positions of three groups of Eastern Kingbirds (*Tyrannus tyrannus*) and Western and Cassin's kingbirds (*T. verticalis* and *T. vociferans*) in spaces defined by PC 1 and PC 2 of principal components analyses of the correlations among the averages of eight variables. The axes are proportional to the eigenvalues of the components.

TABLE 7

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST TWO COMPONENTS FROM PRINCIPAL COMPONENTS ANALYSIS OF MATRICES OF CORRELATIONS AMONG THE MEANS OF EIGHT CHARACTERS FROM THREE SPECIES OF *TYRANNUS*

Character	Males		Females	
	PC 1[a]	PC 2	PC 1	PC 2
Wing length	0.96		0.98	
Outer tail length	0.90	0.42	0.94	0.35
Inner tail length	0.95	0.30	0.99	
Tarsus length	0.83	−0.51	0.95	
Culmen length (total)	0.99		0.99	
Culmen length (from nares)	0.90	−0.42	0.95	
Culmen width (at nares)	0.92	−0.38	0.90	−0.43
Culmen depth (at nares)	0.98		0.96	
Eigenvalue	6.9	0.9	7.3	0.6
Variance explained	86.6%	11.8%	91.6%	7.0%

[a] Correlations <0.30 not printed.

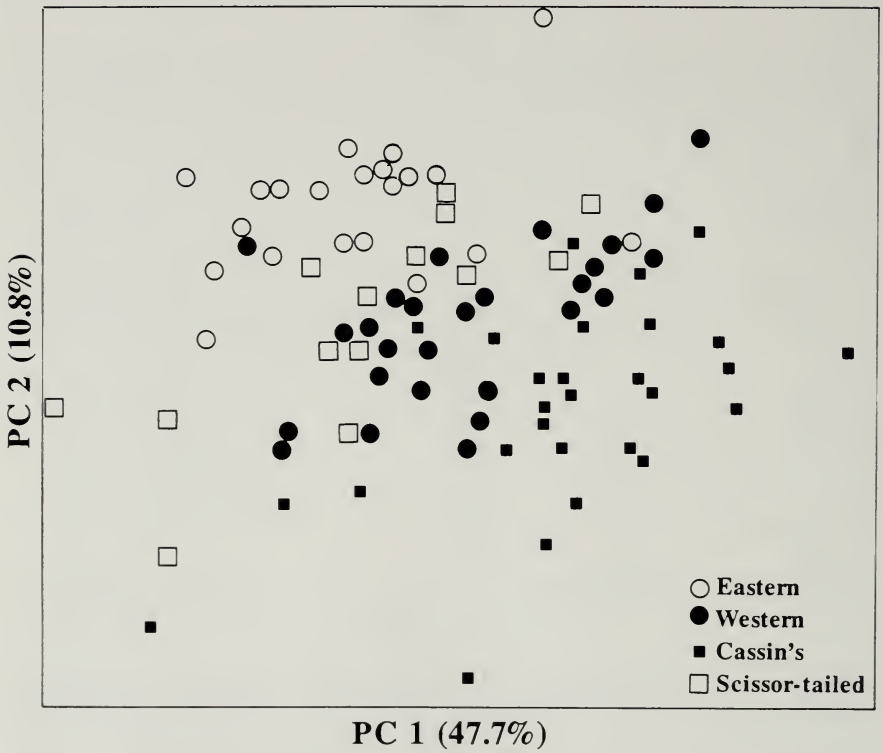

FIG. 5. Two-dimensional plot of the positions of 91 individuals of four taxa of *Tyrannus* from a principal components analysis of the correlations among 27 skeletal characters.

values). Therefore, if character displacement were occurring, we predict that it will be evident in these features in populations of *T. tyrannus* that are sympatric with one or (especially) two other *Tyrannus,* namely *T. verticalis* or both *T. verticalis* and *T. forficatus.*

Geographical trends.—The univariate analyses show that there is little geographic variation in size and there are no clear geographic patterns. In females, seven of the 12 characters measured show statistically significant variation. However, the 10 samples are divided into only two, or at most three (for wing length) statistically homogeneous sets, and there is, in all instances, a great deal of overlap between or among sets. Looking at the characters in concert, there is a tendency for northwestern females (British Columbia, Saskatchewan, and Manitoba) to be larger than eastern ones. Although there is significant geographic variation in 10 of the 14 characters for males, no trends are obvious; there is perhaps a tendency for western birds to be larger than eastern ones. The Mantel's tests revealed

TABLE 8

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST THREE COMPONENTS FROM A PRINCIPAL COMPONENTS ANALYSIS OF CORRELATIONS AMONG THE MEANS OF 27 SKELETAL CHARACTERS OF 19 *TYRANNUS* OF FOUR SPECIES

Character	PC 1	PC 2	PC 3
Skull length	0.77[a]		
Premaxilla length (total)	0.73	−0.48	
Skull width	0.87		
Premaxilla length (nares)	0.71	−0.38	
Premaxilla depth	0.56		
Narial width	0.57		0.39
Premaxilla width	0.68		
Interorbital width	0.41		0.41
Mandible length	0.78	−0.48	
Gonys length	0.60	−0.59	
Mandible depth	0.40	−0.48	
Coracoid length	0.81		
Scaupla length	0.73	0.36	
Femur length	0.84		−0.38
Femur width	0.45		
Tibiotarsus length	0.76		−0.45
Tarsometatarsus length	0.79		−0.45
Humerus length	0.84		
Ulna length	0.72		
Carpometacarpus length	0.82		
Phalanx length	0.59		
Hallux length	0.53		−0.50
Sternum length	0.53	0.61	
Sternum depth	0.52	0.33	0.45
Keel length	0.53	0.51	0.33
Synsacrum width	0.73	0.34	
Synsacrum length	0.61	0.52	−0.31
Eigenvalue	12.3	2.9	2.0
Variance explained	45.7%	10.8%	7.4%

[a] Correlations <0.30 not printed.

a positive, but not significant ($P > 0.05$) relationship between phenotypic (ATD) distance and geographic distance and a significant ($P < 0.01$) negative correlation between the ATD and the reciprocal of geographic distance. Thus, although geographic distance does not predict phenotypic distance, samples from adjacent localities are more similar to each other than would be predicted by chance alone.

These geographic trends are best summarized by the multivariate (PCA) analyses. In the PCA for females, all characters except culmen width and

TABLE 9

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST THREE PRINCIPAL COMPONENTS FROM A PRINCIPAL COMPONENTS ANALYSIS OF A MATRIX OF CORRELATIONS AMONG THE MEANS OF 12 CHARACTERS OF 10 SAMPLES OF FEMALE EASTERN KINGBIRDS

Character	PC 1	PC 2	PC 3
Wing length	0.96[a]		
Wing tip to 10th		−0.77	0.49
Wing tip to 5th	0.73	−0.61	
Wing tip to 4th	0.62	−0.64	
Wing tip to secondary	0.59	0.59	0.34
Outer tail length	0.91		
Inner tail length	0.89		
Tarsus length	0.66		−0.53
Total bill length	0.80	0.35	
Culmen length (from nares)	0.76	0.40	
Culmen width (at nares)			−0.93
Culmen depth (at nares)		−0.75	−0.30
Eigenvalue	5.5	2.7	1.7
Variance explained	46.1%	22.1%	14.3%

[a] Correlations <0.30 not printed.

bill height are correlated positively with PC 1 (the correlation between wing-tip to 10th, however, is small) (Table 9). Thus females with large PC 1 scores are large, with relatively long and thin bills. PC 2 is highly negatively correlated with the three primary wing-tip characters and bill height, and positively correlated with wing-tip to secondary and measures of bill length. Hence, birds with large values for PC 2 have relatively round wings and long, thin bills.

The females from the northwestern part of the range have the largest PC 1 values, thus generally have longer wing, tails and bills than birds from the east, although the sample from Montana is an exception to this trend (Fig. 6). To the extent that PC 1, from this analysis, could be interpreted as a general measure of body size, these data indicate that female Eastern Kingbirds increase in size from east to west. PC 2, which explains an additional 22.1% of the variance, especially separates the samples from northern Ontario and Manitoba from Montana and Saskatchewan.

The PCA for the males shows a similar, although more complicated pattern. PC 1, which explains 42.3% of the total variance, is highly positively correlated with wing length, three of the wing-tip lengths, both tail lengths, tarsus length, and bill length and width (Table 10). Males with

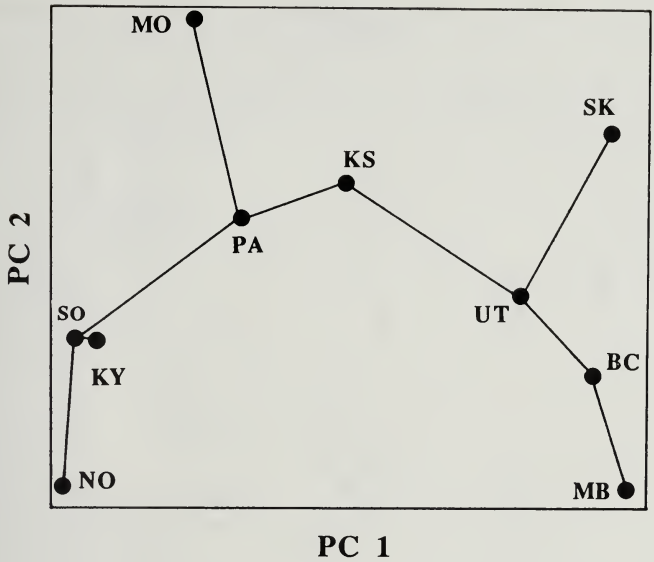

FIG. 6. Two-dimensional plot of the positions of the averages of 10 samples of female Eastern Kingbirds in the space defined by PC 1 and PC 2 from a principal components analysis of the correlations among the means of 12 measurements. PC 1 explains 46.1% of the total variance among the means, and PC 2 explains an additional 22.1%. The locality abbreviations are: BC = British Columbia, KS = Kansas, KY = Kentucky, MB = Manitoba, MO = Missouri, NO = northern Ontario, PA = Pennsylvania, SK = Saskatchewan, SO = southern Ontario, and UT = Utah. Each sample includes birds from states or provinces other than those named.

large values for this component have relatively long and round wings, long tails and tarsae, and large bills, and by these criteria, the males from the west (Manitoba, Wyoming, Nebraska, Alberta, and North Dakota) are the largest. However, birds from Illinois, Ohio, and northern Ontario are nearly as large, whereas birds from North Carolina and Pennsylvania are the smallest, with birds from southern Ontario, British Columbia, and New England being nearly as small (Fig. 7). PC 2, which explains an additional 15.1% of the variation, contrasts wing shape (wing-tip to secondary), bill length and width with tarsus length and bill height, and separates southwestern birds (Utah, Oklahoma, Texas, New Mexico, and Nebraska) from the others (Fig. 7). PC 1 and PC 2, however, together explain just over half of the total variation, and the minimum spanning tree, which summarizes the relationships among the localities in the 14 dimensional space shows some of the distortions in this two dimensional

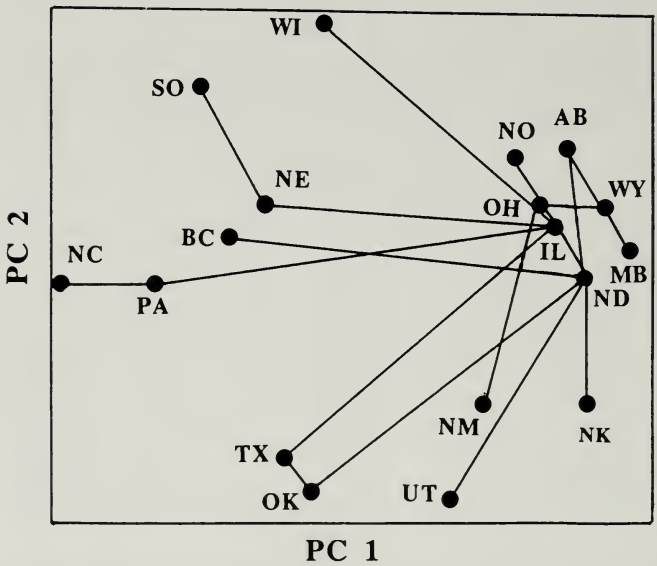

FIG. 7. Two-dimensional plot of the positions of the means of 18 samples of male Eastern Kingbirds in the space defined by PC 1 and PC 2 of a principal components analysis of the correlations among the averages of 14 measurements. PC 1 explains 42.3% of the total variance in the matrix and PC 2 explains an additional 15.1%. The abbreviations for the sample names are: AB = Alberta, BC = British Columbia, IL = Illinois, MB = Manitoba, NC = North Carolina, ND = North Dakota, NE = New England, NK = Nebraska, NM = New Mexico, NO = northern Ontario, OH = Ohio, OK = Oklahoma, PA = Pennsylvania, SO = southern Ontario, TX = Texas, UT = Utah, WI = Wisconsin, and WY = Wyoming.

representation (Fig. 7). For example, British Columbia, which appears to be close to New England and Pennsylvania in the two dimensional space is closer to North Dakota in the 14 dimensional one.

DISCUSSION

Sexual dimorphism.—Although there is no sexual dimorphism in plumage pattern or coloration in Eastern Kingbirds, we find however that there is a significant sexual dimorphism in 10 of 12 measurements. Tarsus length, however, is one of the characters that does not vary with sex. Murphy (1988) likewise found no dimorphism in tarsus length in Eastern Kingbirds from eastern Kansas. If tarsus length is a measure of body size *per se* in kingbirds as suggested elsewhere (Haberman et al. 1991), then there is no sexual dimorphism in size in Eastern Kingbirds. Additionally, although the shape of the outer primaries differs between sexes in *Tyrannus,* there is no dimorphism in distance between the wing tip and the tip

TABLE 10

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST THREE PRINCIPAL COMPONENTS FROM A PRINCIPAL COMPONENTS ANALYSIS OF A MATRIX OF CORRELATIONS AMONG THE AVERAGES OF 14 MEASUREMENTS ON 18 SAMPLES OF MALE EASTERN KINGBIRDS

Character	PC 1	PC 2	PC 3
Wing length	0.93[a]		
Wing tip to 10th			−0.92
Wing tip to 5th	0.88		
Wing tip to 4th	0.95		
Wing tip to secondary		−0.51	0.31
Wing tip length	0.75		
Wing tip width	0.39		0.46
Outer tail length	0.94		
Inner tail length	0.92		
Tarsus length	0.42	0.54	
Total bill length	0.60	−0.48	
Culmen length (from nares)		−0.84	
Culmen width (at nares)	0.56	−0.51	
Culmen depth (at nares)		0.44	−0.58
Eigenvalue	5.9	2.1	1.6
Variance explained	42.3%	15.1%	11.7%

[a] Correlations <0.30 not printed.

of the 10th primary in Eastern Kingbirds. Male Eastern Kingbirds have longer wings, wing tips (distance between the tip of the longest primary, and either the 4th or 5th primary or the longest secondary), tails, and bills than females, but females have more robust bills (larger culmen width and depth). The longer wings, wing tips, and tails of male Eastern Kingbirds probably result from the aerial and visual displays that the males perform during courtship and in territorial defense. Females do not patrol and rarely guard the territory (Smith 1966). Longer wing and tail feathers of males relative to the same body size probably facilitate these displays. It is also possible that they reflect sexual differences in migratory behavior, although no such differences have been reported.

Even though we found sexual dimorphism in bill size, possibly indicating that the sexes feed on somewhat different prey, there is no geographic variation in the extent of bill dimorphism in Eastern Kingbirds. Thus there is no indication that the magnitude of such dimorphism is influenced by interspecific competition, as would be predicted by the niche variation hypothesis (Van Valen 1965, Haberman et al. 1991).

Geographic variation in size and shape.—Although there is significant geographic variation in all of the features that we measured on Eastern

Kingbirds, there are few clear geographic trends. As a general rule, the largest individuals are found in the northern Great Plains (and for females in British Columbia as well), whereas the smallest individuals are found in the east. There is, thus, no indication that this species conforms to the trend described by Bergmann's Rule (James 1970, Zink and Remsen 1986, Aldrich and James 1991). As mentioned above, the species is highly migratory, and leaves North America before the inception of cold weather. Thus the significance of size to thermoregulation (commonly postulated to select for relatively large body size in cold regions) is probably relatively unimportant in these kingbirds. The Eastern Kingbird can be added to the list of migratory species that do not support Bergmann's rule (Zink and Remsen 1986). The absence of any geographic trends in size variation also indicates that there is no interspecific character displacement in Eastern Kingbirds, and the PC analysis likewise gives no indication of character displacement (Fig. 4).

The Eastern Kingbird is multivariately most like the Scissor-tailed Flycatcher of the four *Tyrannus* studied, and least like Cassin's Kingbird. Eastern Kingbirds differ from Scissor-tailed Flycatchers and Western Kingbirds primarily by having smaller bills. There is, however, no evidence of character displacement in bill size in Eastern Kingbirds in populations that are sympatric with one or both of these congeners. This suggests that interspecific niche partitioning is not occurring in North American *Tyrannus*.

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EFFECTS OF BIRD BLOWFLY PARASITISM ON EASTERN BLUEBIRD AND TREE SWALLOW NESTLINGS

DANIEL D. ROBY,[1] KAREN L. BRINK,[2] AND KARIN WITTMANN[3]

ABSTRACT.—Large numbers of bird blowfly (*Protocalliphora*) larvae in nests reportedly cause nestling morbidity and mortality in some host species, but other studies have failed to find significant effects. We conducted controlled blowfly removal and addition experiments to reveal the effects of blowfly infestations on nestling growth, development, and survival of Eastern Bluebirds (*Sialia sialis*) and Tree Swallows (*Iridoprocne bicolor*). Blowflies were found in about 70% of the nests of both species. Intensity of blowfly parasitism averaged 95 blowflies/infested nest. Mean parasite burdens in infested bluebird nests were significantly greater than in swallow nests. The number of nests parasitized and the intensity of blowfly infestations increased significantly during the breeding season. There were no significant differences in nestling survival or fledging age among blowfly removal, addition, and control treatments for either species. Average bluebird nestling mass on day 14 was significantly lower in control nests than in blowfly removal nests, but the difference was small; for swallows, differences in nestling mass among treatments were not significant. Regressions of average nestling mass against mass of blowflies/nestling were significant for bluebirds on day 10 and for swallows on day 14 but explained only 14.5% and 5.5%, respectively, of variation in nestling mass. The effects of blowfly parasitism on reproductive success were minor and apparently exerted little selection pressure for nest dispersion in the two study species. *Received 9 Oct. 1991, accepted 18 April 1992.*

Larvae of the blowfly genus *Protocalliphora* (Diptera: Calliphoridae) are obligate hematophagous parasites on a wide variety of nestling birds (Sabrosky et al. 1989). Most species of bird blowflies are intermittent ectoparasites that live concealed in nest material, rarely are observed obtaining blood meals from nestlings, and obtain most blood meals at night (George and Mitchell 1948, Boyd 1951, Kenaga 1961). Pupation occurs either in the nest or on the ground under the nest. Species of birds that nest in cavities or in nests constructed of mud generally support higher infestations of blowfly larvae (Mason 1944, Pinkowski 1977, Gold and Dahlsten 1983). *Protocalliphora avium* specializes on parasitizing the nestlings of larger, open-nesting hawks, eagles, and owls (Hill and Work 1947, Bohm 1978, Crocoll and Parker 1981). The larvae of *P. avium* live continuously as ectoparasites on the head, neck, and especially in the aural cavities of nestlings (Bortolotti 1985). *Protocalliphora hirudo* is the only member of the genus confirmed to be an obligate subcutaneous

[1] Cooperative Wildlife Research Laboratory and Dept. Zoology, Southern Illinois Univ., Carbondale, Illinois 62901 (Present address: Alaska Cooperative Fish and Wildlife Unit, 209 Irving Building, Univ. of Alaska, Fairbanks, Alaska 99775-0990).
[2] P.O. Box 571, Carbondale, Illinois 62903 (Present address: P.O. Box 900154, Fairbanks, Alaska 99775-1040).
[3] 1709 Beulah Rd., Churchville, New York 14428.

parasite (George and Mitchell 1948, Bédard and McNeil 1979, Garrison et al. 1986), capable of remaining with the host after fledging (but see Halstead 1988).

Bird blowflies have received considerable attention from managers of bluebird nest box trails, whose goal is to maximize production of fledglings from nest boxes. Pupal cases of *Protocalliphora* frequently are encountered in nest boxes after nesting season and blamed for death of nestlings. Low nestling weights, slow development, anemia, and mortality in the nest have all been attributed to blowfly infestations (Henshaw 1908; Johnson 1929, 1930, 1931, 1932; Mason 1936; Kenaga 1961). Recent popular articles blame heavy infestations (>100 larvae) for nestling mortality and recommend treating infested nests with 1% rotenone powder (Zeleny 1986, Audubon Society of New York State 1986).

Despite these reports, several studies have been unable to detect significant nestling mortality as a consequence of *Protocalliphora* infestation, even in cases where the parasite loads were high (Mason 1944, Bennett 1957, Whitworth 1976, Pinkowski 1977, Gold and Dahlsten 1983). However, these were correlational investigations and none included controlled experiments designed to reveal the effects of blowfly infestations on nestlings. In the present study, we investigated the impact of bird blowflies on the growth, development, and survival of nestling Eastern Bluebirds (*Sialia sialis*) and Tree Swallows (*Iridoprocne bicolor*) in artificial nest boxes. Our objective was to gain insight into the effects of blowfly infestations by taking an experimental approach and actively manipulating blowfly parasite burdens in nests. To our knowledge, the present study represents the first experimental attempt to test the hypothesis that bird blowflies have a negative effect on their hosts (Sabrosky et al. 1989).

STUDY AREA AND METHODS

Field work was conducted during the 1987 and 1988 breeding seasons at Genesee Country Museum, Mumford, Monroe County, New York. The study area consisted of ca 480 ha of rolling terrain and varied habitat, including agricultural fields, fallow fields, thickets, second growth hardwood forest, and swampy bottomlands. Forty-seven nest boxes were erected in 1985, prior to initiation of the study. In 1987, a total of 205 nest boxes were in place prior to the onset of nesting, and in 1988 this number increased to 325. Most nest boxes (N = 273) were erected in meadows, fallow fields, and mowed areas at least 30 m from the nearest hedgerow, thicket, or wooded area, with the remainder erected in thickets (N = 24), at the edge of agricultural fields (N = 20), and around the perimeter of a 3-ha lake (N = 8). Nest boxes were erected at 30 m intervals.

Nest boxes were half-gallon paper milk cartons lined on the inside and outside with asphalt roofing felt. We drilled entrance holes (38 mm diameter) near the top edge of the milk carton. Milk cartons were placed in wooden holders consisting of a solid roof, back, and floor with vertical braces on each side. Copper wire stretched across the front of the braces held the milk carton insert in place. This design allowed us to take inserts containing intact

nests to the lab and examine them carefully for parasites. Each nest box was mounted 2 m above the ground on 2.5 cm (1 inch) black steel pipe that was greased to prevent access by climbing predators.

All nest boxes were numbered and checked weekly for nesting activity throughout the breeding season (early April to mid-August). Active bluebird and swallow nests were checked daily during the hatching period to ascertain hatching date. Each bluebird nest that successfully hatched young was alternately assigned to either the control or removal (experimental) treatment. Each swallow nest with young was systematically assigned to either the control, removal, or addition treatment. At 6, 10, and 14 days post-hatching, each nestling was weighed in the field to the nearest 0.25 g using a Pesola spring scale (50 g capacity) and placed in a substitute nest insert lined with tissue paper. The substitute insert was then replaced in the wooden frame to allow the parents to continue caring for nestlings while the nest was searched for parasites. The insert containing the nest was taken indoors where nest materials were emptied into a large tray for examination. We attempted to remove all bird blowflies from nest material, using lepidopterist's tweezers, and placed them in a weighing pan. It proved very difficult to locate and remove all blowfly eggs and first instar larvae from nest material because of their small size (<1.5 mm). Larvae removed from nests were counted and weighed to the nearest 0.1 g on a triple beam balance. Average body mass of blowflies in each nest was estimated by dividing the total mass of blowflies by the number in the nest. When eggs and first instar larvae were detected, they were noted and the number present was estimated.

After removal of blowflies, all nest material was returned to the insert from which it came. Nests were reconstructed by layering the fine nest material on top of the coarse and shaping the material into a cup. Nestlings were sufficiently advanced by six days post-hatching that the minor reduction in insulative quality associated with nest reconstruction was considered inconsequential. For nests in the control group, all blowfly larvae were placed on top of the replaced nest material. These larvae quickly moved out of sight into the nest material. For nests in the removal group, no blowflies were returned to the nest. For nests in the addition group, all blowflies removed from the nest were returned and any blowflies found in a nest from the removal treatment were added. The number and mass of larvae added to nests in the addition group was recorded. Inserts containing the nests were returned to their original location, nestlings were replaced, and the insert replaced in its holder. Nestlings were back in their original nests within 1–2 h of removal.

After nest examination on day 14, each nest was checked daily to determine fledging date. In nests where fledging was asynchronous, the age at which each nestling fledged was used to calculate a mean fledging age. In a few instances it was evident that certain nestlings had fledged prematurely (i.e., disappeared from the nest several days before the other nestlings). Premature fledging can result from the disturbance associated with checking nests. These individuals were not included in the calculation of mean fledging age.

Nestling mortality was recorded if a dead nestling was found in the nest after day 6 or if a nestling disappeared from the nest between day 6 and day 14. By day 10, dead nestlings were apparently too large for parent swallows or bluebirds to remove then from the nest; nestlings older than 10 days that died were invariably found in the nest. Some nestling mortality occurred prior to the day 6 nest examination, usually in the first or second day post-hatching. These losses could not be attributed to blowfly parasitism because of the absence or very small size of any *Protocalliphora* larvae at this stage.

Brood size varied considerably among nests of both study species. The parasite burden experienced by a nestling is dependent on both the total mass of parasites in the nest and the number of brood mates that share that burden. In order to adjust parasite burden for differences in brood size, the mass of blowflies infesting a nest was expressed on a per nestling

basis. Pupae from several bluebird nests were collected after the nestlings had fledged and held until adults emerged. Adults were identified by C. W. Sabrosky and deposited in the insect collection at the Illinois Natural History Survey, Urbana.

Regression analysis and ANOVA were performed using Statworks version 1.0. All analyses involving percentages were performed on arcsine-transformed data. Test statistics were considered significant when $P \leq 0.05$.

RESULTS

Adult flies raised from pupae collected from nest boxes were identified as *Protocalliphora sialia* by C. W. Sabrosky. The limited number of blowfly adults identified to species raises the possibility of infestations of other *Protocalliphora* species or mixed infestations. However, *P. sialia* is a common species infesting Eastern Bluebird and Tree Swallow nests in the Northeast and it is likely that infestations were primarily, if not entirely, of this species (Sabrosky et al. 1989).

A total of 142 nests were included in the study—51 Eastern Bluebird nests and 91 Tree Swallow nests. Of these nests, 99 (69.7%) were infested with blowfly larvae. The prevalence of infestation was slightly higher in bluebird nests (76.5%) than in swallow nests (65.9%), but this difference was not significant ($\chi^2 = 1.719$, $P > 0.05$). Overall prevalence of infestation was somewhat greater in 1987 (84.0%) than in 1988 (62.0%), but this difference was not significant ($\chi^2 = 7.456$, $P > 0.05$) and data from the two years were combined for further analyses.

Parasite numbers in infested, control nests on day 10 post-hatching averaged 95 larvae/nest (SD = 78.8, N = 41). Mean parasite number in 21 infested, control bluebird nests (116 larvae/nest ± 78.9 [SD]) was significantly greater than that of 19 swallow nests (60 larvae/nest ± 47.7, $t = 2.77$, $P < 0.05$). The maximum number of blowfly larvae found in a nest was 284 for bluebird nests and 319 for swallow nests. For infested nests, per nestling parasite burden for bluebird nestlings on day 14 averaged 1.2 g ± 0.96 (N = 36) with a maximum of 3.2 g and for swallows averaged 1.0 g ± 0.74 (N = 52) with a maximum of 2.8 g. These per nestling parasite burdens are equivalent to 4.3% (maximum = 11.7%) and 4.7% (maximum = 12.6%) of average nestling body mass on day 14 for bluebirds and swallows, respectively.

The significantly lower average intensity of parasitism in swallow nests was apparently due to density-dependent factors that affected the size and number of blowflies in nests. In swallow nests, the average mass of blowflies on day 14 was negatively correlated with the number of blowflies in the nest ($r = -0.292$, $P = 0.007$) and positively correlated with swallow brood size ($r = 0.213$, $P = 0.029$). In a multiple regression model, number of blowflies and host brood size explained 15.4% of the variation in

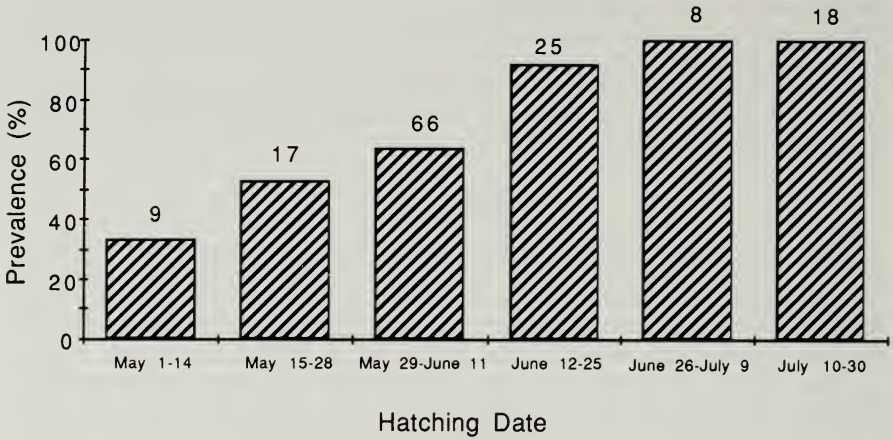

FIG. 1. Seasonal trend in blowfly parasitism in Eastern Bluebird and Tree Swallow nests.

average blowfly mass ($F_{2,61} = 5.53$, $P = 0.006$). Also, in heavily parasitized swallow nests the numbers of blowflies often declined substantially from day 10 to day 14. The change in number of blowflies in control nests from day 10 to day 14 was significantly dependent on the number of blowflies on day 10 ($F_{1,30} = 19.55$, $P < 0.0005$, $r^2 = 0.40$, $b = -0.47$). These results suggest that both the number and size of blowfly larvae in swallow nests were constrained by intraspecific competition for limiting resources.

The prevalence of parasitized nests increased as the breeding season progressed (Fig. 1). Less than half of nests that hatched in May were parasitized (N = 26), while all nests that hatched in July were parasitized (N = 22). Eastern Bluebirds normally raise two broods annually in western New York (D. D. Roby, unpubl. data) and first broods have a lower probability of being infested with blowflies than second broods. Among parasitized bluebird broods, parasite burden per nestling at day 6 increased significantly with Julian hatch date ($F_{1,36} = 6.055$, $P = 0.018$, $r^2 = 0.144$, Fig. 2). Tree Swallows normally raise a single brood in a breeding season. Swallow nests in which eggs hatched before the median hatching date had a significantly lower average parasite burden (49 larvae/nest ± 39.2, N = 31) than those that hatched after the median hatching date (86 larvae/nest ± 63.2, N = 32, $t = 2.802$, $P < 0.05$).

The mean mass of blowfly larvae/nestling on day 6 (before treatment) did not differ significantly among treatment groups for either bluebirds or swallows (Table 1), indicating that treatment groups had similar blowfly burdens up until experimental manipulation of blowflies was initiated on day 6. Removal treatments frequently did not eliminate infestation com-

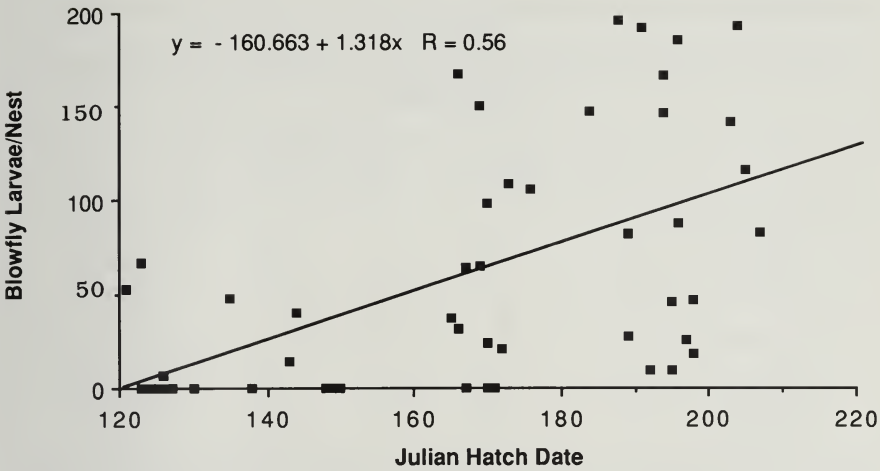

FIG. 2. Seasonal trend in intensity of blowfly parasitism in Eastern Bluebird nests at six days post-hatching.

pletely, as indicated by persistent blowfly burdens on days 10 and 14 (Table 1). This was partly because not all blowfly eggs and first instar larvae were detected and removed on day 6 and, in some cases, reinfestation occurred after removal on day 6. Nevertheless, the average mass of blowflies/nestling on days 10 and 14 in both bluebird and swallow

TABLE 1

AVERAGE MASS[a] (G) OF BIRD BLOWFLY LARVAE PER NESTLING IN EASTERN BLUEBIRD AND TREE SWALLOW NESTS AS A FUNCTION OF TREATMENT

	Age (days after hatching)		
	6	10	14
Eastern Bluebird			
Removal	0.15 (0.165, 25)	0.35 (0.392, 24)	0.32 (0.468, 24)
Control	0.17 (0.235, 26)	1.07 (0.750, 25)	1.44 (1.034, 25)
ANOVA	$F_{1,49} = 0.16$	$F_{1,48} = 8.73$	$F_{1,47} = 23.48$
	$P = 0.693$	$P = 0.005$	$P < 0.0005$
Tree Swallow			
Removal	0.02 (0.043, 29)	0.06 (0.094, 29)	0.15 (0.233, 29)
Control	0.02 (0.049, 32)	0.29 (0.420, 32)	0.76 (0.706, 32)
Addition	0.06 (0.125, 30)	0.50 (0.703, 30)	0.95 (0.878, 30)
ANOVA	$F_{2,88} = 1.843$	$F_{2,88} = 6.04$	$F_{2,88} = 11.44$
	$P = 0.162$	$P = 0.004$	$P < 0.0005$

[a] Mean (SD, N).

TABLE 2

SURVIVAL[a] OF EASTERN BLUEBIRD AND TREE SWALLOW NESTLINGS AMONG BIRD BLOWFLY TREATMENTS

	Nestling survival (%)		
	Mean	SD	N
Eastern Bluebird			
Removal	77.5	35.6	25
Control	87.0	22.1	26
ANOVA	$F_{1,49} = 1.32$	$P = 0.255$	
Tree Swallow			
Removal	97.3	8.2	29
Control	94.3	18.6	32
Addition	89.8	25.6	30
ANOVA	$F_{2,88} = 1.19$	$P = 0.309$	

[a] Percent of nestlings alive on day 6 post-hatching that successfully fledged.

nests was significantly greater for control and addition treatments than for removals (Table 1).

Despite significantly lower parasite burdens in removal treatments, there was no significant difference in nestling survival between treatments for either bluebirds or swallows (Table 2). Also, nestling survival was not significantly dependent on the mass of blowflies/nestling on day 14 for either bluebirds ($F_{1,47} = 0.081$, $P = 0.774$) or swallows ($F_{1,89} = 2.513$, $P = 0.113$). Some bluebird and swallow nests with high per nestling blowfly burdens experienced 100% nestling survival. However, bluebird nestling survival was significantly dependent on the number of blowflies in the nest on day 10 ($F_{1,48} = 9.328$, $P = 0.004$, $r^2 = 0.163$). This significant regression resulted from two nests with the highest blowfly infestations found in bluebird nests. In one nest containing 284 blowfly larvae on day 10, one of four nestlings died on day 16 and the others fledged. In the other nest containing 265 larvae on day 10, three of four nestlings died by day 10 and the fourth was dead by day 14. One of the parents of this brood apparently abandoned the nest, but it is possible that high numbers of blowflies contributed to the death of the entire brood. In the Tree Swallow nest with the highest blowfly infestation (319 larvae on day 10), one of five nestlings was dead by day 10, but the other four fledged.

There were no significant differences in fledging age among treatments for either bluebirds or swallows (Table 3). The regression of fledging age against the mass of blowflies/nestling on day 14 was also not significant for either bluebirds ($F_{1,44} = 0.027$, $P = 0.864$) or swallows ($F_{1,86} = 0.569$, $P = 0.541$).

TABLE 3

FLEDGING AGE OF EASTERN BLUEBIRD AND TREE SWALLOW NESTLINGS AMONG BIRD BLOWFLY TREATMENTS

	Fledging age (days after hatching)		
	Mean	SD	N
Eastern Bluebird			
Removal	18.0	1.66	21
Control	18.0	1.65	25
ANOVA	$F_{1,44} = 0.01$	$P = 0.940$	
Tree Swallow			
Removal	19.4	1.25	29
Control	19.8	1.36	31
Addition	19.7	1.53	28
ANOVA	$F_{2,85} = 0.596$	$P = 0.558$	

The effect of blowfly parasitism on nestling body mass was investigated by calculating average nestling mass for each brood on day 10 and day 14. Average nestling mass on day 10 was not significantly different among treatments for either bluebirds or swallows (Table 4). However, average bluebird nestling mass on day 14 was significantly less for control broods compared with broods in the blowfly removal group (Table 4). Average

TABLE 4

AVERAGE MASS[a] (G) OF EASTERN BLUEBIRD AND TREE SWALLOW NESTLINGS AMONG BIRD BLOWFLY TREATMENTS

	Age (days after hatching)		
	6	10	14
Eastern Bluebird			
Removal	16.3 (2.12, 24)	25.2 (3.03, 24)	28.2 (1.73, 23)
Control	16.0 (2.96, 25)	24.3 (3.51, 25)	27.0 (2.48, 25)
ANOVA	$F_{1,47} = 0.22$ $P = 0.647$	$F_{1,48} = 1.37$ $P = 0.246$	$F_{1,46} = 4.13$ $P = 0.045$
Tree Swallow			
Removal	13.2 (1.95, 29)	20.9 (1.86, 29)	22.5 (1.60, 29)
Control	13.0 (2.26, 32)	20.5 (2.21, 32)	22.1 (1.97, 32)
Addition	12.9 (2.12, 30)	19.9 (2.78, 30)	21.4 (2.29, 30)
ANOVA	$F_{2,88} = 0.11$ $P = 0.898$	$F_{2,88} = 1.58$ $P = 0.211$	$F_{2,88} = 2.71$ $P = 0.070$

[a] Mean (SD, N).

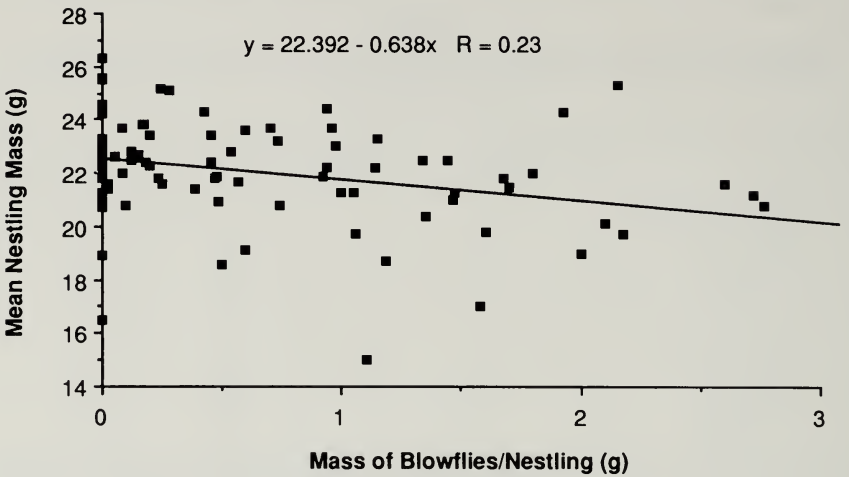

FIG. 3. Average mass of Tree Swallow nestlings at 14 days post-hatching as a function of per nestling burden of blowflies.

bluebird nestling mass on day 14 was 1.2 g (4.3%) lower in the control group compared with the removal group. Average swallow nestling mass on day 14 was lowest in the addition group and highest in the removal group, but differences were small and marginally nonsignificant (Table 4).

We further investigated the relationship between nestling mass and parasite burden by regressing average nestling mass against the mass of blowflies/nestling. For bluebirds, this regression was significant on day 10 ($F_{1,47} = 8.001$, $P = 0.007$, $r^2 = 0.145$), but not significant on day 14 ($F_{1,46} = 0.91$, $P = 0.652$). The significant regression on day 10 was due to a single nest where three of four nestlings had died, leaving the lone survivor in a nest containing 265 blowflies with a combined mass of 8.4 g. For swallows, the regression of nestling mass against per nestling mass of blowflies was not significant on day 10 ($F_{1,89} = 2.38$, $P = 0.123$), but was significant on day 14 ($F_{1,89} = 5.20$, $P = 0.023$, b = −0.64, SE = 0.28). However, per nestling blowfly burden explained only 5.5% of the variation in swallow nestling mass, and other factors were responsible for most of the variation in nestling mass (Fig. 3).

DISCUSSION

Differences in nestling growth, development, and survival between blowfly treatments were either nonsignificant or only marginally significant. Even in cases where parasite burdens were unusually high, effects of blowfly parasitism on nestling survival and mass (Fig. 3) were not pronounced. The few nests where blowfly parasitism may have caused

nestling mortality were late nests, when the prevalence and intensity of blowfly parasitism were greatest. Also, brood sizes for late nests were generally lower, contributing to higher per nestling parasite burdens late in the breeding season.

These experimental results are consistent with previous correlational studies that failed to detect higher nestling mortality associated with blowfly parasitism (Bennett 1957, Whitworth 1976, Pinkowski 1977, Gold and Dahlsten 1983). It is possible that small reductions in nestling mass, such as those found in this study, may have a significant effect on fledging mass and post-fledging survival. But loss of blood to blowfly larvae normally declines prior to fledging, as larvae enter a prepupation stage, and ceases abruptly when fledglings leave the nest. Consequently, nestling recovery from the effects of blowfly parasitism may occur prior to or shortly after fledging.

Several investigators have speculated that, even in the absence of overt signs of impact on nestlings, blowfly infestations would be expected to contribute to nestling mortality during periods of food stress or adverse weather (Whitworth 1976, Gold and Dahlsten 1983). In the present study, the incidence of nestling starvation and brood reduction was relatively high in Eastern Bluebird nests, compared with Tree Swallow nests (Table 2). Most mortality of bluebird nestlings was associated with periods of cool, rainy weather, and mortality occurred in unparasitized as well as parasitized nests. While the survival of swallow nestlings was not significantly different among treatments, there was a trend toward lower means and higher variances in nestling survival with increasing parasite burden (Table 2). Consequently, a larger sample of swallow nests might reveal a significant effect of blowfly parasitism on nestling survival. This was not expected because mean intensity of blowfly infestations was considerably lower for swallow nests than for bluebird nests (Table 1).

Ectoparasites that live in nests have recently received attention from avian ecologists seeking to understand the relationship between nest dispersion and fitness (Hoogland and Sherman 1976, Brown and Brown 1986, Shields and Crook 1987). Using controlled experiments, Brown and Brown (1986) demonstrated that infestations of the swallow bug (*Oeciacus vicarius*) significantly lowered nestling body mass and nestling survival in the highly colonial Cliff Swallow (*Hirundo pyrrhonota*). Because the number of swallow bugs per nest was positively correlated with colony size, these parasites represent a cost to coloniality in Cliff Swallows. Similarly, Shields and Crook (1987) found parasitism by the bird blowfly *Protocalliphora hirundo* to be a major source of mortality for nestling Barn Swallows (*H. rustica*), a facultatively colonial species. Parasite numbers were positively correlated with colony size and negatively correlated

with reproductive success, again suggesting a substantial cost to coloniality. Our results indicate that the effects of blowfly parasitism on reproductive success of Eastern Bluebirds and Tree Swallows are small and do not constitute an appreciable selection pressure for nest dispersion beyond current spacing. Unfortunately, nearest neighbor distances for active swallow and bluebird nests were not recorded in the present study, so it is not possible to test the hypothesis that proximity to an infested nest increased the probability of infestation in new nests. However, Tree Swallows nested semi-colonially in some fields within the study area, whereas active bluebird nests were more dispersed. Despite the greater dispersion of bluebird nests, prevalence of parasitism was not significantly different in nests of the two species, and intensity of parasitism was higher in bluebird nests than in swallow nests. These results suggest that nest dispersion had little effect on parasite burdens.

The small magnitude or complete absence of treatment effects on nestling survival, fledging age, or body mass raises the question of how blowfly parasitism can incur such minor costs for hosts. One factor contributing to the low pathogenicity of bird blowfly parasitism for Tree Swallow nestlings was the presence of density-dependent feedback on the size and number of larvae in nests, limitations that apparently mitigate the impact of blowflies on hosts. Although density-dependent feedback on the size and number of larvae was not as evident in bluebird nests, there was some evidence that the number of larvae in nests was constrained. For two bluebird nests in the blowfly removal treatment, a total of 471 and 467 blowfly larvae, respectively, were removed over the course of the nestling period. These numbers far exceeded the maximum number of larvae found in control nests at any one time (284 larvae), indicating that considerable mortality of larvae can occur at high densities. The results suggest that density-dependent constraints on blowflies would limit parasite burdens below the level where nestling mortality occurs, even if the two study species nested colonially.

Another potential explanation for the small effect of bird blowflies on their hosts is that the quantity of blood lost may be small relative to nestlings' tolerance for blood loss and hematopoietic capacity. If host nestlings mount little or no immune response to blowfly parasitism, the costs to hosts would be limited to replacing lost blood. No measurements of blood consumption rates are available for *Protocalliphora,* but some simple calculations will reveal the magnitude of potential blood loss. Bird blowfly larvae progress through three instars, totaling 11–13 days, prior to the prepupation stage, and the first two instar stages are relatively short (Sabrosky et al. 1989). The nestling period from day 6 to day 14 generally coincided with the third instar stage, when most larval growth takes place.

During this period, the mean mass of individual blowflies increased from 10 mg to 75 mg, or a growth increment of 65 mg. If we assume that blowfly larvae are 40% efficient at converting blood meals to biomass (Gold and Dahlsten 1983), then each larva consumed ca 160 mg of blood, or ca 20 mg of blood/day. Consequently, a 10-day-old swallow nestling in a nest of average brood size (4.4 nestlings) and with an average parasite burden (60 larvae) lost ca 270 mg of blood/day, or 1.3% of average body mass. A 10-day-old bluebird nestling in a nest of average brood size (3.4 nestlings) and with an average parasite burden (116 larvae) lost ca 680 mg of blood/day or 2.8% of average body mass. Blood volume in nestling passerines is ca 10% of body mass (Sturkie 1986:106), so these daily blood loss estimates are equivalent to 13% and 28% of total blood volume, respectively. These estimates of blood loss for average broods with average parasite burdens are not trivial, particularly for bluebird hosts, but estimates of blood loss for heavily parasitized broods are substantially higher. In the case of the swallow nest with the heaviest infestation of blowflies (319 larvae), the estimate of daily blood loss was 1.5 g/nestling, or ca 75% of total blood volume/day. In the case of the bluebird nest with the heaviest infestation of blowflies (284 larvae), the estimate of daily blood loss was 1.3 g/nestling, ca 50% of total blood volume/day.

It is difficult to conceive of how nestlings can tolerate blood loss of this magnitude for long. Birds, unlike mammals, can survive the loss of most of their blood volume (e.g., 70% of blood volume during prolonged hemorrhage in pigeons, Jones and Johansen 1972). Nevertheless, it is clear that blowfly parasitism can result in the loss of significant quantities of blood by nestlings of the two study species. The small effect of bird blowflies on their hosts is not adequately explained as a consequence of the quantity of blood lost to these parasites. The remarkable tolerance of nestling bluebirds and swallows to chronic blood loss warrants further investigation.

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BODY COMPOSITION, FAT RESERVES, AND FASTING CAPABILITY OF CAPE GANNET CHICKS

René A. Navarro[1]

Abstract.—Age-related changes in lipid, water, and non-lipid content and energy density of four major body parts (integument, viscera, leg and pectoral muscles, and carcass) of Cape Gannet chicks, juveniles, and adults were studied. The proportion of water was typically high for neonates and decreased during development to near adult levels at fledging. The percentage of lean dry matter remained almost constant for muscles and carcass but decreased in viscera and integument due to fat deposited during growth. Energy density was linearly related to age (kJ/g = 4.46 + 0.076 Age (days), $r^2 = 0.845$, $P < 0.001$). Fasting capability (FC) of chicks (survival time when using only their lipid reserves, calculated from lipid mass and field metabolic rate) increased exponentially up to 70 days of age ($FC = 0.6e^{0.05\ Age}$, $r^2 = 0.815$, $P < 0.001$). Newly fledged birds have a fasting capability between 8–16 days and adults only 1–2 days. Time between consecutive feeds, from field observations at the nest, for chicks 21–40, 41–60 and 61–80 days old were 11.9 ± 0.7 h, N = 74; 16 ± 1.1 h, N = 50; and 20 ± 0.6 h, N = 35, respectively. The results are contrary to the hypothesis that fat deposits are an insurance against an unpredictable fast, although they may serve for this purpose. Fat deposits may be the physiological consequence of the temporal pattern of feeding by adults, or they may serve as energy sinks to increase energy requirements relative to the nutrient and protein requirements of chicks. *Received 16 May 1991, accepted 23 Mar. 1992.*

Seabirds share a number of characteristics that set them apart from most other birds such as low clutch size, deferred maturity and slow chick growth. It is thought that these characteristics are related to the unpredictable, patchy, and fluctuating nature of the food resources that seabirds exploit. Lack (1968) proposed that due to a limitation in the ability of adults to supply food, the pattern of development of the chicks is characterized by slow growth and the accumulation of large fat deposits. These fat deposits are interpreted as an insurance against the poor feeding conditions occasionally experienced by adults when foraging at sea (Lack 1968). Two predictions that can be drawn from Lack's hypothesis are tested in this paper: (1) a close match between fasting capability (i.e., fat deposits) and maximum time between consecutive feeds should be expected, and (2) assuming that the lean dry mass is well regulated by controls on somatic growth, the fat deposits should exhibit some variability as a consequence of chicks consuming their fat deposits during fast periods, so it is reasonable to expect a higher variance in fat deposits than in lean dry mass. On the other hand, Ricklefs (1979) suggests that pro-

[1] Percy FitzPatrick Institute of African Ornithology, Univ. of Cape Town, Rondebosch 7700, South Africa (Present address: Bird Atlas Project, Dept. of Statistical Sciences, Univ. of Cape Town, Rondebosch 7700, South Africa).

longed and unpredictable fasting is not the main force acting upon selection for large fat deposits in seabird chicks but that it may be a by-product of the energy-rich and nutrient-poor diet of most seabirds. Large fat deposits thus may be accumulated by seabird chicks as energy sinks to allow the chick to increase its energy requirements relative to the requirements of protein and other nutrients (Ricklefs 1979). Also, chicks are apparently fed more regularly than has been presumed (e.g., Ricklefs et al. 1985, Stempniewicz and Jezierski 1987, Taylor and Konarzewski 1989). In this case there is no reason to expect a close relationship between lipid deposits and fasting time, and variances of lipid and lean dry matter should be similar.

Gannets and boobies (Sulidae) are large altricial seabirds (Nelson 1978). Chicks are cared for intensively by both parents at the nest for 11 weeks (Peruvian Booby *Sula variegata*) to more than 20 weeks (Abbott's Booby [*Sula abbotti*]), with most species attending the young for ca 13 weeks. Post-fledging care is a characteristic of boobies but not of gannets (Nelson 1978). Growth of sulid chicks has been described for all species, but such studies have traditionally emphasized ontogenetic changes in body mass, and wing and culmen length. Changes in body composition and energy requirements have been studied only in Northern Gannets ([*Sula bassanus*]; Montevecchi et al. 1984), although energetic requirements for growth of Cape Gannets (*Morus capensis*) have been studied by Cooper (1978). In this paper, I describe age-related changes in lipid, water and non-lipid content and energy density of four major body parts (integument, internal organs, leg and pectoral muscles, and carcass) of Cape Gannet chicks, juveniles, and adults. Field data for foraging rate are also analyzed to test predictions from Lack's (1968) hypothesis (see above).

METHODS

Body composition.—Analysis of body composition of Cape Gannets was based on 21 chicks, two fledglings caught two days after fledging, and three adults caught at the end of the breeding season. Birds were collected, under permit, at Malgas Island (33°03′S, 17°55′E), South Africa, between 1987–1989 and kept frozen until analysis. Thawed birds were dissected into four major components: integument (skin plus down, feathers removed), viscera (all internal organs, stomach contents removed), leg muscles plus pectoral muscles, and carcass. Each of the four body components was ground and homogenized and then air-dried at 50°C to constant mass. Wet and dry masses were obtained. Dried material was powdered (or ground and homogenized when fat content was too high), and two aliquots for fat analysis were taken. Lipid content was determined by hexane extraction (2 g of dried material in 25 ml of hexane) for 45 min at 70°C and then centrifuged. From the liquid phase, 2 ml were dried for 30 min at 100°C, and the residues weighted. This method extracts mainly triglycerids and other nonpolar lipids. Phospholipids and cholesterol are not removed by hexane extraction (Fishing Industry Research Inst., UCT, pers. comm.).

The following definitions are used in this paper: water = wet mass − dry mass; lipid =

dry mass × extracted mass/aliquot mass; lean wet mass = wet mass − lipid; lean dry mass = dry mass − lipid; lipid index = lipid/lean dry mass; and water index = water/lean dry mass. Energy equivalents of tissue were calculated using the conversion factors: 38 kJ g^{-1} lipid and 20 kJ g^{-1} lean dry matter (Ricklefs 1974).

Fasting capability.—Fasting capability of birds relying solely on their lipid stores was calculated based on a field metabolic rate (FMR) of 1264 kJ/day for chicks, and FMR = 3380 kJ/day for adults (Adams et al. 1991). For fledglings the FMR of adults was used, though it may underestimate their fasting capability. It was also assumed that the lipid mass equivalent to lipid index of 0.1 was not available for energy generation (Taylor and Konarzewski 1989). This figure was derived from body composition analysis of adult birds of different species starved to death. Such analysis showed the presence of a petroleum ether-extractable material equal to 0.5–2% of the wet body mass that gives lipid indices lower than 0.1 (Evans 1969, Chaplin 1974, Wishart 1979, Jenni and Jenni-Eiermann 1987).

Time between consecutive feedings.—For chicks older than 20 days, adult arrival at the nest after a foraging trip was used as an estimate of time between two consecutive feeds, since feeding of chicks older than 20 days is almost exclusively associated with the arrival of a bird at the nest. Data for two all-day watches of a group of nests (chicks aged 30–60 days) support this assumption: of 39 arrivals witnessed, 36 (92.3%) were followed by chick feeding within 30 min, three did not involve chick feeding and two cases of chick feeding were not associated with adult arrival. Parents usually feed the chick between 1–5 times within 30 min of arrival, but for the purpose of the present analysis, this was considered as a single feeding bout.

Data on adult arrival at the nest were obtained by regularly checking a group of nests every 30 min during daylight hours (and in two opportunities, every 1 h during the night). The time of arrival of a bird was recorded to within 30 min. Birds were dye-marked to recognize members of a pair. These observations were carried out for two to four days consecutively at different stages of chick development. Overnight observations revealed that no shifts at the nest or mate arrival occurred at night.

Unless otherwise stated, variations about means are given as the standard error followed by the sample size.

RESULTS

Body composition.—Changes in water, lipid, and lean dry matter for muscles, viscera, integument, and remaining carcass are shown in Fig. 1. During the nestling period, pectoral and leg muscles were characterized by a large proportion of water (80.2 ± 0.5%, N = 21) and lean dry matter (17.9 ± 0.8%), and small amounts of lipid (1.9 ± 0.1%). The carcass had a similar pattern, the average composition being 73.5 ± 1.0%, 23.2 ± 0.7% and 3.3 ± 0.4% of water, lean dry matter and lipid, respectively. These proportions were different for the integument (63.1 ± 2.7%, 18.9 ± 1.0% and 17.9 ± 2.5% of water, lean dry matter, and lipid, respectively) and viscera (73.5 ± 1.7%, 17.0 ± 0.6% and 9.5 ± 1.7% of water, lean dry matter and lipid, respectively). The proportion of lipid content in pectoral and leg muscles, carcass, internal organs, and integument (4.7 ± 1.8% N = 2, 5.7 ± 1.3%, 32.4 ± 13% and 53.5 ± 3.9%, respectively) of fledglings were markedly higher than those in adults (3.6 ± 1.8% N = 3, 2.6 ± 0.2%, 4.3 ± 0.4% and 18.7 ± 1.6%, respectively). The proportion

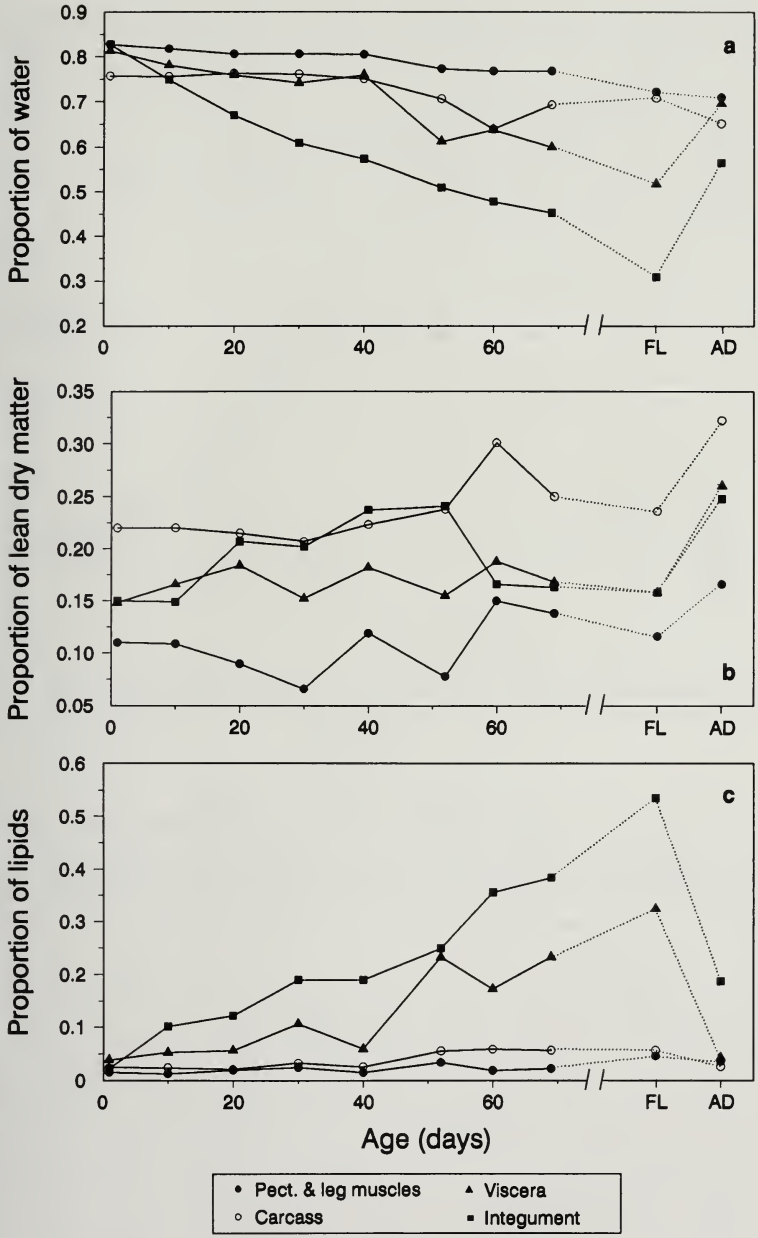

FIG. 1. Changes in lipid (L), lean dry mass (LF) and water (W) content of four major body parts of Cape Gannet chicks as function of age. Contents of fledglings (FL) and adults (AD) are also indicated. Sample sizes are as follows (age:N): 1:3; 10:3, 20:3; 30:3; 40:4; 52: 1; 60:3; 69:1; FL:2; and AD:3.

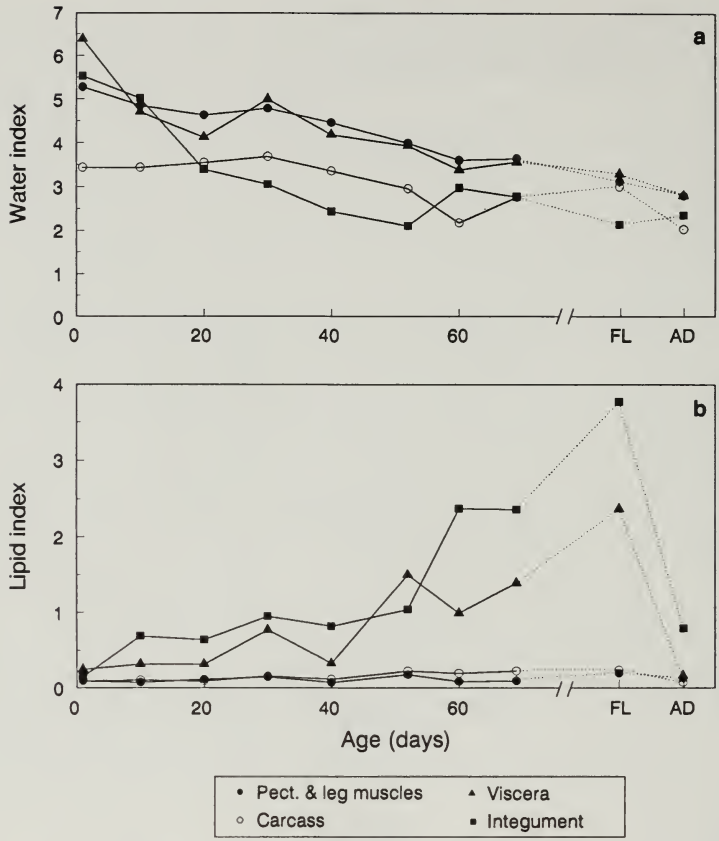

FIG. 2. Relative changes of (a) water index (water g/lean dry matter g) and (b) lipid index (lipid g/lean dry matter g) of four major body parts of Cape Gannet chicks as function of age. Figures for fledgling (FL) and adults (AD) are indicated. Sample sizes as in Fig. 1.

of lean dry matter of pectoral and leg muscles and carcass remained almost constant throughout the nestling period (Fig. 1b).

Water index (which is independent of the fatness level) decreased and approached adult levels in all four major body parts (Fig. 2a). The water index of the neonate (whole chick) is 4.0, which is similar to those of precocial species (range 3 to 4) (Ricklefs et al. 1980). Among the major body parts analyzed, only the viscera are within the range of altricial species (6 to 8), whereas the integument and leg plus pectoral muscles are between the range of precocial and altricial birds. The steady decrease in the water index is directly proportional to an increase in its functional maturity (Ricklefs 1979).

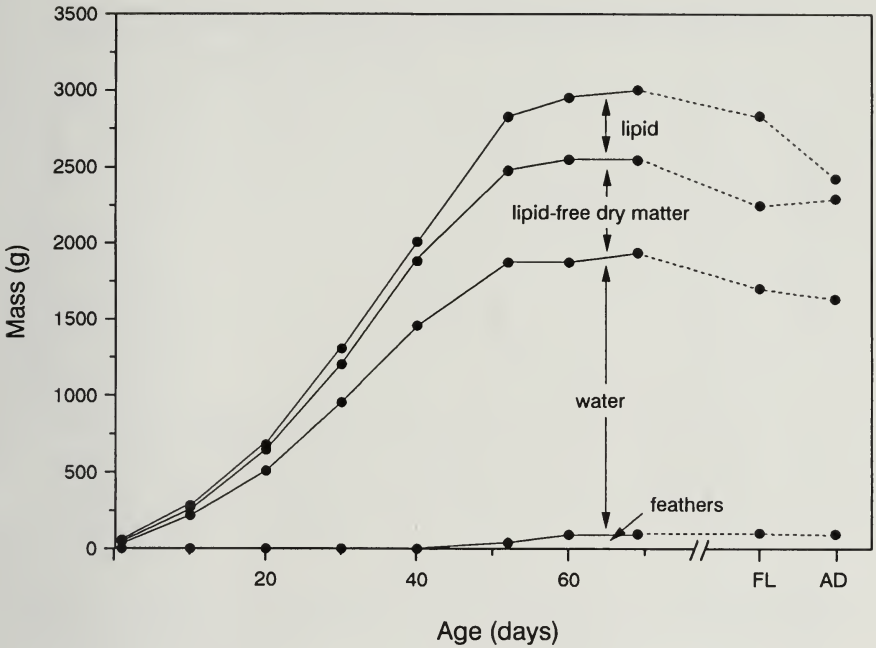

FIG. 3. Overall changes in feathers, water, lean dry matter, and lipid content of Cape Gannet chicks as function of age. Contents for fledgling (FL) and adults (AD) are indicated. Sample sizes as in Fig. 1.

Lipid index (Fig. 2b) increased steadily during chick growth for the integument and viscera, reaching a maximum value in fledglings, whereas it remained more and less constant for pectoral and leg muscles and carcass.

Overall increases in water, lipid, and lean dry matter are shown in Fig. 3, and the energy equivalents of these components are illustrated in Fig. 4a. The energy density (Fig. 4b) was lineally related to chick age (kJ/g = 4.46 + 0.076 (SE = 0.008) Age (days), $r^2 = 0.845$, N = 21, $P < 0.001$). The relationship for the North Atlantic Gannet (kJ/g = 3.35 + 0.16Age) (Montevecchi et al. 1984) was significantly different (ANCOVA: $F_{\text{slopes}[1,31]} = 56.9$, $P < 0.001$; and $F_{\text{adjusted means}[1,31]} = 38.7$, $P < 0.001$; homogeneity of variances test, $F_{\text{max}[2,19]} = 0.79$, $P > 0.05$). The energy density of adults (7.5 ± 0.2, N = 3) was similar to that of a 40-day-old chick, which is ca 58% of the figure reported by Montevecchi et al. (1984) for the North Atlantic Gannet. The lipid fraction accounted for ca 45–65% of the energy stored in the tissues of 50–70-day-old chicks and ca 65% of that of fledglings, but only 27% of adults.

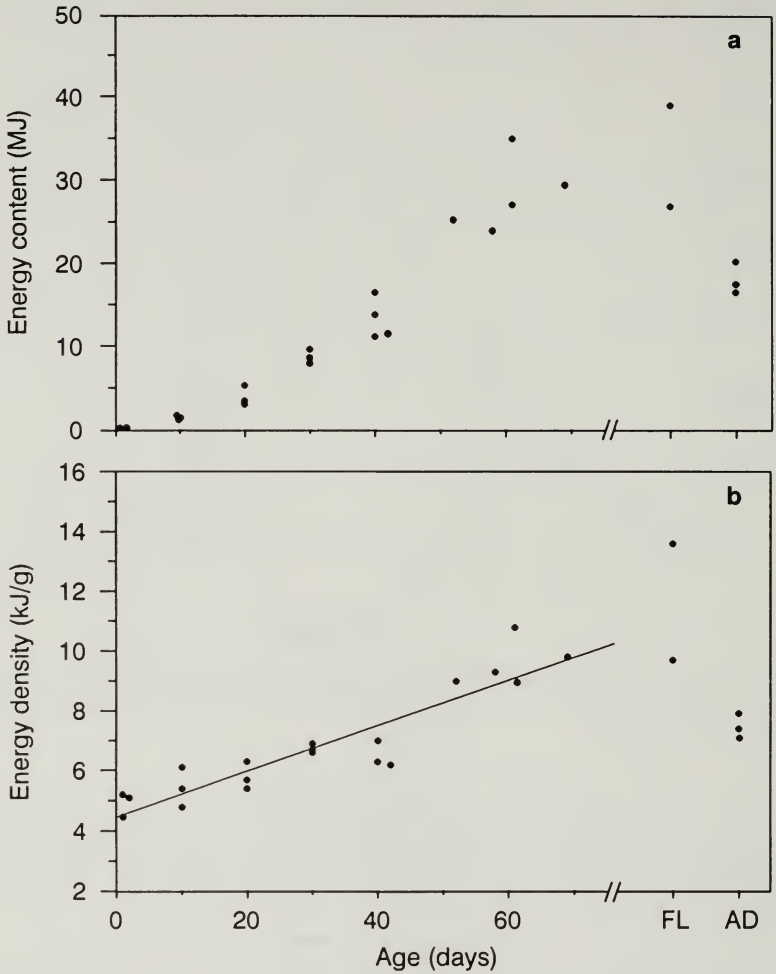

FIG. 4. Changes in (a) energy content and (b) energy density (kJ/g) of Cape Gannet chicks as function of age. Contents for fledglings (FL) and adults (AD) are indicated.

The variances of lipid and lean dry matter of chicks 20–70 days old were compared, after adjusting for their magnitude, by dividing each value by its respective sample mean. This ensures that both data sets have the same mean so that the variances can be compared using a simple ratio. The variance ratio lipid/lean dry matter was $0.764/0.259 = 2.945$, $F_{0.025[14,14]} = 2.983$ (two-tailed test), indicating that the variances were not significantly different.

Fasting capability.—Fasting capability (FC) of chicks increased expo-

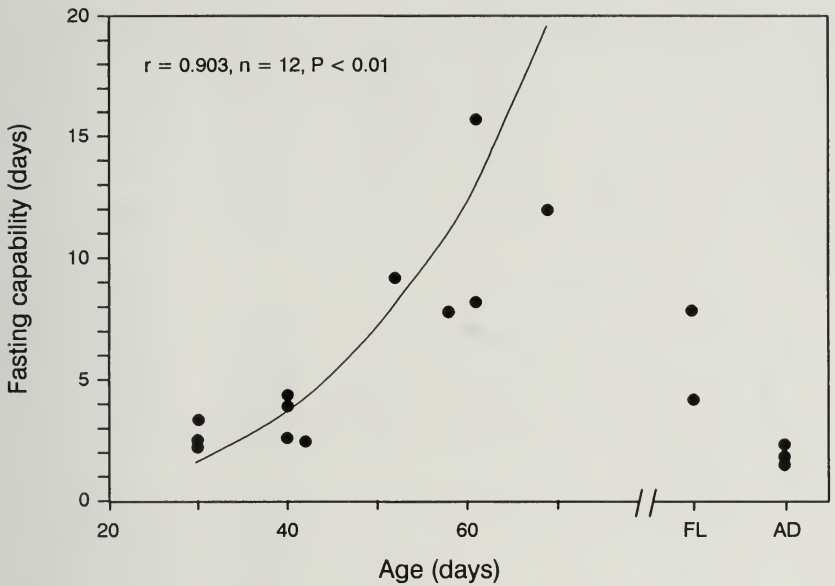

FIG. 5. Estimated fasting capability of chicks, fledglings, and adults assuming that they rely solely on their lipid stores. See text for details of calculations.

nentially up to 70 days of age according to the model: $FC = 0.6e^{0.05Age}$ ($SE_b = 0.01$; $r^2 = 0.815$; N = 12; $P < 0.01$) (Fig. 5). The fat deposits of chicks aged 30–40 days would supply their energetic needs for 2–4.5 days, for chicks 50–70 days old the fat deposits would last for 8–16 days. The two fledglings analyzed had reserves to last them for 4–8 days, whereas lipid reserves of adults would provide them with energy for, at most, one or two days (Fig. 5).

Time between consecutive feedings.—Frequency distribution of time between consecutive feedings for three age classes are shown in Fig. 6. The longest period recorded was 31 h for a 70-day-old chick. The peculiar frequency distribution for chicks 61–80 days old is due to the two adults arriving at the nest within a few hours of each other after long foraging trips (typically >18 h), thus producing the peak observed at ≤6 h. The mean time between feeds for chicks 21–40, 41–60 and 61–80 days old were 11.9 ± 0.7 h, N = 74; 16.0 ± 1.1 h, N = 50; and 17.5 ± 1.2 h, N = 44 (20.0 ± 0.6 h, N = 35 excluding short intervals), respectively. When compared with the fasting capability of chicks (Fig. 5), it is clear that chicks had substantially more fat reserves than were needed to survive the observed intervals between consecutive feedings.

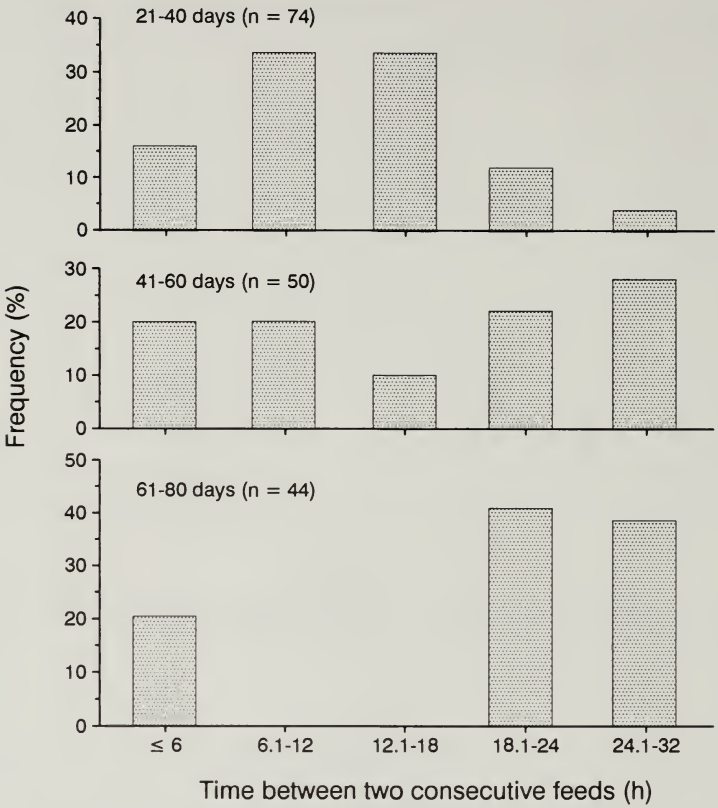

FIG. 6. Frequency distribution of time between two consecutive feedings for three age classes of Cape Gannet chicks.

DISCUSSION

Kirkham and Montevecchi (1982) distinguish three stages of energy partitioning in North Atlantic Gannet nestlings that are also clearly discernible in Cape Gannet chicks. During the first stage, spanning the initial five weeks, the energy delivered to chicks is used primarily for internal organ, skeletal, and muscular development. During this stage, chicks achieve thermal independence and have reached nearly adult dimensions. The second stage covers the period from about the 5th to the 10th week of the nestling period. At this stage, energy is used primarily for feather development and the deposition of substantial fat reserves. There is little development during the final stage which covers the last five weeks of the nestling period. Wings, feathers and pectoral muscles reach maturation, and chicks usually lose mass during this stage.

Adults typically lost mass during the breeding season (pers. obs.), and this must be reflected in their fat deposits. Adults were lean, and their small fat reserves would given them energy for two days at most. Adams et al. (1991), using the doubly labeled water technique, found that, at least during part of the breeding period, adults have a negative energy balance.

Lipid reserves of chicks, expressed as fasting capability, show that they greatly surpass what is required for potential needs, particularly so for chicks older than 50 days. Similar results have been reported previously for other seabirds, e.g., Sooty Tern (*Sterna fuscata*) (Ricklefs and White 1981), Leach's Storm-petrel ([*Oceanodroma leucorhoa*] Ricklefs et al. 1981), North Atlantic Gannet (Montevecchi et al. 1984), and Little Auk (*Alle alle*) (Taylor and Konarzewski 1989). These studies and my results support Ricklefs' (1979) hypothesis that large fat deposits may serve as energy sinks, increasing the chick's energy requirements relative to its requirements of protein and other nutrients, rather than as insurance against unpredictable fasting as proposed by Lack (1968). Occasionally, feeding frequencies could be greatly decreased (e.g., by bad weather spells) or the food provided by parents could be of low calorific value; in such cases fat deposits can make the difference between surviving or not. The adaptive significance lies in the frequency of such events.

Schaffner (1990) suggested that a feeding regime characterized by large but infrequent meals may be the main cause of large fat deposits. Intermittent feeding in poultry resulted in increased lipogenesis, lowered basal metabolic rates and slower growth (e.g., Cohn 1963, Nir et al. 1979).

Even if fat deposits are not crucial for nestlings, in terms of being an energy source, they may be important for juveniles. Recently fledged gannets must rely solely on their reserves until they learn the necessary skills to capture (by plunge-diving) enough food to balance their negative energy budget. In fact, the highest mortality reported for Cape Gannets occurs soon after fledging (Oatley et al. 1992) and it is related to the chick mass at fledging (Jarvis 1974). This factor may also have helped to shape patterns of growth of seabirds, favouring selection of large fat deposits. However, many seabirds loose part of their large fat reserves during a pre-fledgling fast (Lack 1968), indicating that lower body mass is required for efficient flight. Obviously, a fledging bird must compromise between flight efficiency and energy reserves.

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THE EFFECT OF HURRICANE HUGO ON BIRD POPULATIONS ON ST. CROIX, U.S. VIRGIN ISLANDS

ROLAND H. WAUER[1] AND JOSEPH M. WUNDERLE, JR.[2]

ABSTRACT.—Bird populations were sampled along road transects eight months after Hurricane Hugo struck St. Croix, at sites previously sampled on similar dates in 1987. Surveys revealed 33 species both before and after the hurricane, of which 30 species were detected during both samples. However, the average number of birds per stop was significantly lower after the storm's passage than before. No pattern was evident in the changes of aquatic species, but this may reflect limited sample sizes. Among terrestrial species, higher proportions of nectarivores and fruit/seedeaters declined than insectivores or raptors, suggesting that the storm's greatest stress occurred after its passage rather than during its impact. Populations of the Pearly-eyed Thrasher (*Margarops fuscatus*) declined on one transect and increased on another, a pattern consistent with inter-habitat migration. The fruit/seed diet, low population size, and restriction to remnant forest fragments of the Bridled Quail-Dove (*Geotrygon mystacea*) may explain the significant population decline of this species and its disappearance from traditional sites. *Received 9 Jan. 1992, accepted 15 April 1992.*

Hurricanes can have both direct and indirect effects on bird populations. Direct effects involve death from exposure to high winds and rain (Kennedy 1970). Indirect effects include destruction of food supplies or nesting, roosting, and foraging substrates by high winds (Jeggo and Taynton 1980, Engstrom and Evans 1990). Storm-weakened birds may be at greater risk to predation, particularly in the absence of vegetative cover or roosting sites for protection (Engstrom and Evans 1990). Normal migration patterns may be disrupted and, in some instances, change the geographic distribution of species (Thurber 1980). Furthermore, populations may increase in some habitats as a result of increased wandering, migration into new habitats, or the descent of canopy dwellers to ground level (Dunning and Watts 1991, Wunderle et al. 1992). Thus, if hurricanes occur frequently, as in the Caribbean, they may be important factors in determining some of the characteristics of the local avifauna (Wunderle et al. 1992).

Our study takes advantage of pre-hurricane baseline censuses of bird populations conducted along four roadside transects throughout 1987, prior to the arrival on 17 Sept. 1989 of Hurricane Hugo on the Caribbean island of St. Croix in the U.S. Virgin Islands. The baseline censuses were

[1] 202 Padre Lane, Victoria, Texas 77901.
[2] Institute Of Tropical Forestry, Southern Forest Experiment Station, U.S.D.A. Forest Service, P.O. Box B, Palmer, Puerto Rico 00721. (Author to whom all correspondence should be sent.)

replicated eight months after the storm (May 1990) to evaluate its short-term effects on bird populations. This enabled us to document the response of bird populations to the direct impact of a very powerful storm (category 4 on the Saffir-Simpson scale of 5, Brennan 1991) on a relatively small (210 km^2), low lying (max. elevation 353 m) island which has been extensively deforested (Fig. 1).

STUDY SITES AND METHODS

The senior author conducted point counts along roadside transects in four locations on St. Croix in 1987 and 1990. Four transects were selected along roads in rural areas, and stop sites along each transect were selected on the basis of accessibility and representation of habitat types. In 1987, topographic and cultural features and habitat characteristics were mapped for the area within approximately 122 m of each stop. Percentages of habitat types were derived later by placing a square mylar sheet over each map and counting the number of squares representing each type. Habitat classification follows Forman (1980) and reveals that the four transects were dominated by pasture/field (37%), thorn woodland (20%), deciduous forest (12%), semi-evergreen forest (10%), coastal hedge/grassland (6%), littoral woodland (5%), urban (4%), water (3%), cactus scrub (2%), and mangrove woodland (1%). However, the distribution of habitat types was not evenly distributed among the transects, as summarized below:

(A) The south shore transect (16.1 km, N = 25 stops; Fig. 2) follows St. Croix's south-central shoreline (Highway 60), beginning at the junction of the Grassy Point side-road and ending at the entrance to Cane Garden. The route is entirely within the subtropical dry forest life zone (Ewel and Whitmore 1973) with the following habitat types: pasture/field (56%); littoral woodland (12%); thorn woodland (11%); cactus scrub (7%); urban (7%); coastal hedge/grassland (5%); water (1%); and mangrove woodland (<1%).

(B) The north shore transect (11.3 km, N = 21 stops) follows the north-central shoreline (Highway 80), beginning at the junction of Highway 75 and ending at the junction with Highway 73. The route passes through the subtropical dry forest life zone (Ewel and Whitmore 1973) and includes the following habitat types: thorn scrub (34%); coastal hedge/grassland (18%); water (11%); pasture/field (10%); littoral woodland (9%); semi-evergreen forest (9%); deciduous forest (5%); mangrove woodland (2%); and urban (2%).

(C) The Castle Burke transect (8.1 km, N = 16 stops; Fig. 3) crosses St. Croix south to north at mid-island and runs through both the subtropical moist forest and subtropical dry forest life zones (Ewel and Whitmore 1973). It begins at the junction of Centerline Road (Highway 70) and Golden Grove Road and ends at the junction of Highways 69 and 80. The predominant habitat type here is pasture/field (48%); thorn woodland (23%); deciduous forest (17%); semi-evergreen forest (8%); urban (3%); and water (<1%).

(D) The moist forest transect (9.7 km, N = 23 stops; Fig. 4) runs through the northwest mountains and includes the Creque Dam Scenic Road. The route begins at the entrance to the Springfield Quarry on Mahogany Road (Highway 76) and ends at the junction of Creque Dam Road and Northside Drive (Highway 63). The route, within the subtropical moist forest life zone (Ewel and Whitmore 1973), includes pasture/field (38%); deciduous forest (23%); semi-evergreen forest (22%); thorn woodland (11%); urban (4%); and water (<1%).

Censuses were conducted by driving the transect routes during early morning, starting about 15 minutes before sunrise and ending before 07:45 h AST. No censuses were taken on mornings with excessive wind or rain. All birds were counted during a three-minute interval at each stop. The methods followed those of the "Breeding Bird Survey" (Robbins

FIG. 1. Salt River Mangrove Swamp habitat. Upper 1987 photo illustrates mature mangrove forest. Lower 1990 photo illustrates post-Hugo conditions; most mangroves were flattened and the deciduous forest habitat on adjacent hillsides was damaged but recovered much faster.

FIG. 2. South shore. Upper 1987 photo is of typical pasture near center of south shore route. Lower photo illustrates 1990 post-Hugo conditions.

FIG. 3. Castle Burke Pond. Upper 1987 photo is of mature semi-evergreen forest vegetation around pond edge. Lower 1990 photo illustrates post-Hugo habitat.

FIG. 4. Moist forest habitat. Upper 1987 photo illustrates gallery-forest conditions along the western end of Creque Dam Road. Lower photo is of 1990 post-Hugo habitat.

and Van Velzen 1967) with the exception that less than 50 stops were censused per route because of limited distances. Counts were taken bi-weekly throughout 1987 and two to three times in 1990.

Post-hurricane censuses, using the same methods established in 1987, were made between 6–18 May 1990 at the peak of the breeding season. Each transect was replicated on three non-consecutive mornings, except for the Castle Burke transect which was sampled on only two non-consecutive mornings. For each of the corresponding transects, post-hurricane results were compared with the closest pre-hurricane sample dates (22 April–30 May 1987). For each stop along a transect, we calculated the average (based on N = 3 or N = 2 replicated dates) number of birds detected before the storm and the average number detected after the storm. These values were then averaged to provide the mean number of birds per stop for each transect both before and after the storm. The distribution of total individuals among the stops on each transect was normal both before and after the hurricane, enabling us to use paired *t*-tests (Sokal and Rohlf 1981) to compare the pre- and post-hurricane averages of total individuals per stop. However, for over half the species, the distribution of individuals among the stops was not normally distributed. We therefore used nonparametric Mann-Whitney *U*-tests (Sokal and Rohlf 1981) to compare the pre- and post-hurricane distributions for individual species. A probability of type I error of 0.05 or less was accepted as significant, but we show greater values for descriptive purposes.

For each transect, we tallied the number of terrestrial species showing increases, no change, or decreases in average number of detections following the hurricane. Each species was classified as either a nectarivore, frugivore/seedeater, insectivore, or raptor on the basis of Wetmore (1916) and Faaborg (1985). This information was then analyzed in a row × column test of independence with a *G*-statistic (Sokal and Rohlf 1981).

RESULTS

The average number of individual birds per stop, across all transects (N = 85 stops), was significantly lower after the hurricane than before (Table 1). However of the four individual transects, a significant decline (paired *t*-test, df = 24, $t = 8.62$, $P < 0.001$) was detected only on the south shore transect. Here, the decline was greater for terrestrial than for aquatic individuals. On the north shore transect, a significant increase was found in the average number of aquatic birds per stop, but the average for terrestrial birds was unchanged.

Wauer found 33 species (11 aquatic/22 terrestrial) on transects before the hurricane and 33 species (13 aquatic/20 terrestrial) afterwards (see Appendix I for scientific names). Thirty species were encountered both before and after, providing a turnover of three species detected only before and three species detected only after the hurricane. Of the species found only before the hurricane, the Green-backed Heron was rare (N = 1), the Antillean Crested Hummingbird was common and widespread (detected outside the transects after the hurricane), and the Bridled Quail-Dove was uncommon (max count = 5) and confined to the moist forest. The three species found only after the storm were all aquatic and occurred in low numbers (Pied-billed Grebe, N = 1; White-cheeked Pintail, N = 2; Common Moorhen, N = 3).

TABLE 1

CHANGES IN MEAN NUMBER OF INDIVIDUALS (± SE) PER STOP AND TOTAL NUMBER OF SPECIES ON FOUR TRANSECTS ON ST. CROIX BEFORE AND AFTER HURRICANE HUGO

Transect	Individuals per stop[a]		Total number of species	
	Before	After	Before	After
Castle Burke				
Aquatic	0.50 ± 0.30	0.25 ± 0.22	3	3
Terrestrial	23.40 ± 5.12	16.81 ± 0.97	18	17
South shore				
Aquatic	1.52 ± 0.36	1.32 ± 0.51	10	10
Terrestrial	19.61 ± 1.18	10.35 ± 0.81*	20	18
North shore				
Aquatic	0.14 ± 0.09	0.44 ± 0.15*	5	6
Terrestrial	12.81 ± 1.3	12.14 ± 1.18	19	17
Moist forest				
Aquatic	0.00 ± 0.00	0.01 ± 0.01	0	1
Terrestrial	18.54 ± 0.77	17.26 ± 0.75	17	17
Mean total	19.01 ± 1.22	14.80 ± 0.53*	33	33

[a] Mean ± SE; Aquatic and terrestrial individuals in each transect were compared with a paired *t*-test, * = $P < 0.05$.

When making a large number of statistical comparisons, some observations are expected to deviate significantly from expected value by chance alone. We performed 106 individual Mann-Whitney *U*-tests for population changes after the hurricane of which 10% (11) and 5% (5) are expected by chance at significance levels of 0.10 and 0.05, respectively. However, we found that 29 populations changed at $P \leq 0.10$ and that 22 populations changed at $P \leq 0.05$ (Appendix I). Furthermore, six populations showed changes at the level of 0.001, a very unlikely random event. Therefore, most of the population changes after the hurricane are not artifacts of the large number of comparisons.

Seventeen species showed significant or suggestive ($P \leq 0.10$) declines in mean number of individuals per stop on one or more of the transects (Appendix I). The number of suggestive or significant declines was greatest on the south shore transect (N = 14) followed by the moist forest transect (N = 5), north shore (N = 4), and Castle Burke (N = 1). These declines could result from either hurricane-induced mortality, movement to other habitats, or decreases in detectability.

Five species showed significant or suggestive increases in mean number of individuals per stop on one or more transects (Appendix I). Increasing

populations (at $P \leq 0.10$) were most common on the moist forest transect (N = 4), followed by the north shore (N = 1), and Castle Burke transects (N = 1), and South Shore (N = 0). These increases could result from movement into a habitat, or because the birds were easier to detect as a result of vegetation damage.

Two species decreased along some transects and increased along others (Appendix I). Such observations are consistent with a migration explanation, but factors such as changes in detectability could also be involved.

For terrestrial species, we expected the pattern of population decline to vary with diet, with those species relying directly on plants for food most likely to decline. To examine this possibility, species were classified into four diet categories, and the number of populations that decreased was compared to those that either increased or showed no change. Pearly-eyed Thrashers, as extreme diet opportunists (McLaughlin and Roughgarden 1989), could not easily be placed in any of these categories, and therefore were excluded from the initial analysis. A significant interaction between diet type and population trend was found in the remaining populations along the four transects ($G = 10.81$, df = 3, $P = 0.013$), indicating that nectarivores and fruit/seedeaters were more likely to have declining populations than insectivores or raptors. Declines were found in 92% of the nectarivore populations (N = 12), 70% of the fruit/seedeater populations (N = 30), 58% of the insectivore populations (N = 24), and 25% of the raptor populations (N = 8) along the four transect routes.

The finding that terrestrial bird populations relying on plants for food were more likely to suffer declines than those relying on animals was quite robust, regardless of how the Pearly-eyed Thrasher is classified. For example, assuming thrashers are predators results in significantly more declines ($G = 7.04$, df = 1, $P = 0.008$) in populations of primary consumers (76%; 32/42) than secondary consumers (47%; 17/36). Even if thrashers are classified as frugivores, significantly ($G = 3.81$, df = 1, $P = 0.05$) more populations of primary consumers declined (72%; 33/46) than secondary consumers (50%; 16/32).

Previous studies have shown that apparent population increases after hurricanes may result from the presence of canopy dwellers foraging at ground level where they are easier to detect (Wunderle et al. 1992). To examine this possibility we classified all non-raptorial terrestrial species as either canopy dwellers or as ground/understory foragers (foraging on or within 1 m of the ground) on the basis of our previous observations. An analysis of population trends based on foraging site indicates that 37% of the canopy foragers (N = 41 populations) showed increasing populations, as did 31% of the ground/understory populations (N = 29 popu-

lations). Thus, population increases after the hurricane could not be attributed solely to an increase in canopy dwellers at ground level.

DISCUSSION

As Hurricane Hugo approached St. Croix, the storm's forward speed slowed to 14.5 kph over a twelve-hour period, thereby prolonging the exposure of the island to the storm's fury (Brennan 1991). The eye of the storm crossed the southwestern coastline of St. Croix near Frederiksted at about 02:00 h AST on 18 September 1989. After the storm, trained observers deduced from the damage, including the entire island's vegetation, which was literally stripped bare, that all of St. Croix experienced the storm's maximum winds (estimated at 226 kph). Given the island's relatively small size and limited topographic relief it is unlikely that any major natural "refugia" existed which might have harbored bird populations or their food supplies.

All transects received the full impact of the storm, with vegetation damage most severe in areas with tall-stature vegetation, and least severe in the open habitats. Subjective assessments of vegetation damage were not necessarily accurate predictors of the storm's impact on bird populations. For example, population declines were most frequent and often most severe on the south shore transect, which contained the highest percentage of pasture (56%). Even though declines here were also less severe in secondary than in primary consumers, 83% (5/6) of insectivores declined. For some species (e.g., Gray Kingbird) open pastures may have been a habitat in which most population declines were attributable to mortality due to the direct effects of the storm, rather than to resource shortages in its aftermath.

Semi-evergreen and deciduous forests suffered extensive structural damage, as sampled along the moist forest transect and parts of the Castle Burke transect. Yet these transects had the lowest percentages of populations with declining population trends (Castle Burke 58%; moist forest 45%) and several species showed suggestive ($P < 0.10$) or significant ($P < 0.05$) population increases. Population increases associated with major structural damage to tall-stature forests were found in Jamaican mangroves and wet limestone forest after Hurricane Gilbert (Wunderle et al. 1992) and in the El Verde rainforest in Puerto Rico, immediately after the passage of Hurricane Hugo (Waide 1991). There population increases in storm-damaged forests have been attributed to increased detectability, wandering, migration, and the presence of canopy dwellers foraging at ground level. Our results suggest that the latter was probably not important in contributing to the population increases observed on St. Croix.

Our results are consistent with studies that indicate that population declines in the aftermath of hurricanes are most likely among nectarivores and fruit/seedeaters and less likely among insectivores or raptors. Recent hurricane studies have documented this pattern in sites with varying degrees of vegetation damage in a diversity of habitats, including lowland rainforests of Nicaragua (Boucher 1990), subtropical dry forests in the Yucatan (Lynch 1991), montane habitats in Jamaica (Wunderle et al., 1992), subtropical wet forest in Puerto Rico (Waide 1991), subtropical dry forest on Guadeloupe (Bénito-Espinal and Bénito-Espinal 1991), and subtropical dry woodland and subtropical moist forest on St. John (Askins and Ewert 1991). These results are not unexpected given that hurricane winds strip flowers, fruits, and seeds from plants, which often require many months or even years for recovery (Wunderle, unpubl. data). In contrast, some arthropod populations are unaffected by the storm, and those that are affected often have high recovery rates (Wolcott 1932). In some instances, major outbreaks of arthropods have occurred in the aftermath of hurricanes (Torres, in press).

Some insectivore declines did occur (e.g., Black-whiskered Vireo, Mangrove Cuckoo, Yellow Warbler), particularly if their foraging substrates had been lost. The massive mortality of mangroves undoubtedly contributed to the Yellow Warbler's decline. In contrast, on Jamaica the number of Yellow Warblers had increased in surviving mangrove remnants four months after the hurricane's passage (Wunderle et al. 1992). In this species, moderate to high levels of vegetation damage (stem and branch breakage) contribute to higher local population densities concentrated in relatively intact remnant vegetation, but outright tree mortality (trunk snaps or uprooting) results in population decline. For insectivores whose foraging substrates were not lost, such as Cattle Egrets, the storm had no effect on the number of individuals observed at foraging sites. However, Cattle Egrets were largely absent from their traditional roost site at Castle Burke Pond where more than 100 egrets regularly roosted in large trees prior to the destruction of the site.

One species that may not have survived the hurricane or its aftermath is the Bridled Quail-Dove, a previously rare, fruit/seedeater that was confined to remnant forest fragments on St. Croix. This quail-dove was not detected on our transects after the hurricane, and a search at another traditional site at Caledonia Gut also failed, despite the production of low whistle sounds that previously had evoked responses. Bridled Quail-Doves appear to be sensitive to openings in the forest canopy, as demonstrated by the related Ruddy Quail-Dove (*Geotrygon montana*), which disappeared from areas with extensive canopy damage in the aftermath of Hurricane Hugo in the Luquillo Experimental Forest in Puerto Rico

(Waide 1991). In Puerto Rico, Ruddy Quail-Doves persist in undamaged patches of forest scattered throughout continuous forest (11,330 ha), and in other forest reserves that were unaffected by the storm. In contrast, on St. Croix Bridled Quail-Doves were locally confined to small remnant forest fragments. Extensive damage to these fragments left the species with few, if any, potential refugia, thereby increasing the likelihood of local extinction. A similar scenario (severe fragmentation of the habitat of a forest-dwelling fruit/seedeater followed by hurricane impacts) may have contributed to the extinction of the Puerto Rican Bullfinch (*Loxigilla portoricensis grandis*) on St. Kitts (Raffaele 1977), and is likely to be more common in the future as habitat fragmentation continues in hurricane-prone regions.

Many of the hurricane's effects observed in the St. Croix avifauna were also noted by Askins and Ewert (1991) on the nearby island of St. John (64 km north), which was out of the storm's main path and suffered considerably less damage. St. John's forest was extensively defoliated, with frequent broken branches and occasional treefalls. Despite the relatively light damage on St. John, Askins and Ewert also observed the pattern of diet-related population declines, with significant reductions in the numbers of Scaly-naped Pigeon, Antillean Crested Hummingbird, Bananaquit, and Pearly-eyed Thrasher in either moist forest or dry woodlands. These authors also documented an increase in Northern Waterthrushes (*Seiurus noveboracensis*), suggesting movement into a habitat from a badly damaged site elsewhere. Thus even with relatively light storm damage, population declines can occur due to mortality or emigration from the disturbed site.

Despite Hurricane Hugo's tremendous force and the extensive damage to St. Croix, terrestrial bird population declines were still primarily related to diet, indicating that the hurricane's greatest stress occurred after its passage rather than during its impact. Therefore the ability to use a variety of disturbed habitats appears to be a key predictor of post-hurricane survival in many terrestrial birds. Indeed, most of the terrestrial species on St. Croix (with the exception of Bridled Quail-Doves) are common in a variety of human-disturbed habitats, and thus it is not surprising that most survived this destructive storm with reasonably intact populations. Most of the bird species that occur on St. Croix are widespread geographically in the Caribbean and their ability to use various disturbed habitats has probably facilitated their survival in this hurricane-prone region.

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Appendix I

Mean (± SE) Number of Individuals per Stop before (Upper Row) and after (Lower Row) Hurricane Hugo on Four Transects on St. Croix[a]

Species	Diet	Transect			
		Castle Burke	South shore	North shore	Moist forest
Pied-billed Grebe		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
(*Podilymbus podiceps*)		0.06 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Brown Pelican		0.38 ± 0.23	0.01 ± 0.01	0.02 ± 0.02	0.00 ± 0.00
(*Pelecanus occidentalis*)		0.00 ± 0.00	0.11 ± 0.05	0.06 ± 0.04	0.00 ± 0.00
Magnificent Frigatebird		0.00 ± 0.00	0.67 ± 0.19	0.02 ± 0.02	0.00 ± 0.00
(*Fregata magnificens*)		0.00 ± 0.00	0.69 ± 0.50	0.06 ± 0.04	0.00 ± 0.00
Great Blue Heron		0.03 ± 0.03	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
(*Ardea herodias*)		0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
Great Egret		0.06 ± 0.04	0.16 ± 0.05	0.00 ± 0.00	0.00 ± 0.00
(*Casmerodius albus*)		0.16 ± 0.13	0.11 ± 0.05	0.10 ± 0.07	0.01 ± 0.01
Little Blue Heron		0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
(*Egretta caerulea*)		0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.02	0.00 ± 0.00
Cattle Egret	I	8.59 ± 4.59	0.96 ± 0.25	0.02 ± 0.02	0.03 ± 0.02
(*Bubulcus ibis*)		1.28 ± 0.45	1.52 ± 0.34	0.57 ± 0.25*	0.64 ± 0.22*
Green-backed Heron		0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00
(*Butorides striatus*)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
White-cheeked Pintail		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
(*Anas bahamensis*)		0.00 ± 0.00	0.03 ± 0.03	0.00 ± 0.00	0.00 ± 0.00
Red-tailed Hawk	R	0.06 ± 0.04	0.00 ± 0.00	0.03 ± 0.33	0.06 ± 0.03
(*Buteo jamaicensis*)		0.03 ± 0.03	0.01 ± 0.01	0.33 ± 0.03	0.16 ± 0.07
American Kestral	R	0.03 ± 0.03	0.05 ± 0.03	0.00 ± 0.00	0.00 ± 0.00
(*Falco sparverius*)		0.03 ± 0.03	0.01 ± 0.01	0.02 ± 0.02	0.04 ± 0.03

APPENDIX I
CONTINUED

Species	Diet	Transect			
		Castle Burke	South shore	North shore	Moist forest
Helmeted Guineafowl	F	0.00 ± 0.00	0.81 ± 0.80	0.00 ± 0.00	0.00 ± 0.00
(*Phasianus meleagris*)		0.00 ± 0.00	0.44 ± 0.31	0.32 ± 0.03	0.03 ± 0.03
Common Moorhen		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
(*Gallinula chloropus*)		0.03 ± 0.03	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
Killdeer		0.00 ± 0.00	0.11 ± 0.05	0.00 ± 0.00	0.00 ± 0.00
(*Charadrius vociferus*)		0.00 ± 0.00	0.05 ± 0.03	0.00 ± 0.00	0.00 ± 0.00
Black-necked Stilt		0.00 ± 0.00	0.05 ± 0.03	0.00 ± 0.00	0.00 ± 0.00
(*Himantopus mexicanus*)		0.00 ± 0.00	0.05 ± 0.04	0.00 ± 0.00	0.00 ± 0.00
Laughing Gull		0.00 ± 0.00	0.13 ± 0.09	0.00 ± 0.00	0.00 ± 0.00
(*Larus atricilla*)		0.00 ± 0.00	0.13 ± 0.09	0.00 ± 0.00	0.00 ± 0.00
Royal Tern		0.00 ± 0.00	0.24 ± 0.21	0.00 ± 0.00	0.00 ± 0.00
(*Sterna maxima*)		0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.06	0.00 ± 0.00
Least Tern		0.00 ± 0.00	0.12 ± 0.05	0.10 ± 0.07	0.00 ± 0.00
(*Sterna antillarum*)		0.00 ± 0.00	0.12 ± 0.05	0.14 ± 0.08	0.00 ± 0.00
Rock Dove	F	0.00 ± 0.00	0.04 ± 0.04	0.02 ± 0.16	0.00 ± 0.00
(*Columba livia*)		0.25 ± 0.25	0.27 ± 0.03	0.00 ± 0.00	0.00 ± 0.00
Scaly-naped Pigeon	F	2.59 ± 0.36	0.07 ± 0.04	1.56 ± 0.41	3.51 ± 0.32
(*Columba squamosa*)		2.16 ± 0.32	0.00 ± 0.00	1.06 ± 0.22	2.81 ± 0.31
White-crowned Pigeon	F	0.00 ± 0.00	0.09 ± 0.04	0.13 ± 0.11	0.00 ± 0.00
(*Columba leucocephala*)		0.00 ± 0.00	0.01 ± 0.01*	0.37 ± 0.21	0.00 ± 0.00
Zenaida Dove	F	0.97 ± 0.23	1.67 ± 0.41	1.46 ± 0.23	1.42 ± 0.17
(*Zenaida aurita*)		1.31 ± 0.26	0.69 ± 0.17*	1.32 ± 0.21	1.54 ± 0.17
Common Ground-Dove	F	0.84 ± 0.19	3.32 ± 0.51	0.43 ± 0.12	0.81 ± 0.16

Appendix I
Continued

Species	Diet	Transect			
		Castle Burke	South shore	North shore	Moist forest
(*Columbina passerina*)		0.69 ± 0.18	0.85 ± 0.15*	0.11 ± 0.06*	0.64 ± 0.14
Bridled Quail-Dove	F	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.05
(*Geotrygon mystacea*)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00*
Mangrove Cuckoo	I	0.22 ± 0.09	0.15 ± 0.04	0.33 ± 0.07	0.22 ± 0.07
(*Coccyzus minor*)		0.19 ± 0.08	0.05 ± 0.02	0.02 ± 0.02*	0.10 ± 0.05
Smooth-billed Ani	I	0.03 ± 0.03	0.73 ± 0.20	0.02 ± 0.02	0.20 ± 0.10
(*Crotophaga ani*)		0.34 ± 0.17	0.52 ± 0.12	0.13 ± 0.07	0.30 ± 0.12
Green-throated Carib	N	0.03 ± 0.03	0.07 ± 0.03	0.02 ± 0.02	0.00 ± 0.00
(*Eulampis holosericeus*)		0.00 ± 0.00	0.00 ± 0.00*	0.00 ± 0.00	0.01 ± 0.01
Antillean Crest. Humm.	N	0.19 ± 0.08	0.22 ± 0.10	0.95 ± 0.41	0.19 ± 0.10
(*Orthorhyncus cristatus*)		0.00 ± 0.00*	0.00 ± 0.00*	0.00 ± 0.00*	0.00 ± 0.00*
Caribbean Elaenia	F	0.25 ± 0.11	1.08 ± 0.20	0.49 ± 0.14	0.22 ± 0.12
(*Elaenia martinica*)		0.47 ± 0.21	0.88 ± 0.22	0.48 ± 0.12	0.71 ± 0.24
Gray Kingbird	I	3.53 ± 0.42	2.47 ± 0.18	2.02 ± 0.29	2.28 ± 0.24
(*Tyrannus dominicensis*)		3.22 ± 0.44	1.57 ± 0.19*	2.00 ± 0.28	2.52 ± 0.23
Northern Mockingbird	F	0.31 ± 0.11	0.87 ± 0.12	0.10 ± 0.07	0.03 ± 0.02
(*Mimus polyglottos*)		0.22 ± 0.11	0.13 ± 0.05*	0.00 ± 0.00	0.00 ± 0.00
Pearly-eyed Thrasher	F	1.56 ± 0.29	0.19 ± 0.05	2.31 ± 0.51	6.13 ± 0.37
(*Margarops fuscatus*)		2.66 ± 0.38*	0.37 ± 0.11	2.87 ± 0.54	4.48 ± 0.26*
Black-whiskered Vireo	I	0.91 ± 0.16	0.72 ± 0.09	0.60 ± 0.16	0.51 ± 0.13
(*Vireo altiloquus*)		1.21 ± 0.18	0.37 ± 0.06*	0.48 ± 0.14	0.68 ± 0.14

Appendix I
Continued

Species	Diet	Transect			
		Castle Burke	South shore	North shore	Moist forest
Yellow Warbler	I	1.06 ± 0.24	2.49 ± 0.22	1.21 ± 0.26	0.65 ± 0.18
(*Dendroica petechia*)		1.00 ± 0.18	1.65 ± 0.20*	1.03 ± 0.21	0.65 ± 0.19
Bananaquit	N	1.56 ± 0.26	2.31 ± 0.21	1.51 ± 0.19	2.03 ± 0.23
(*Coereba flaveola*)		0.69 ± 0.16*	0.75 ± 0.13*	1.05 ± 0.12*	1.58 ± 0.17
Black-faced Grassquit	F	0.66 ± 0.16	1.36 ± 0.18	0.60 ± 0.14	0.16 ± 0.07
(*Tiaris bicolor*)		1.13 ± 0.26	0.51 ± 0.11*	0.57 ± 0.17	0.36 ± 0.09

[a] Number of stops per transect are as follows: Castle Burke (N = 16); South shore (N = 25); North shore (N = 21); Moist forest (N = 23). Diet is classified for terrestrial foragers: F = fruit or seed; N = nectar; I = insect, O = omnivore; R = raptor. Significant differences ($P < 0.05$) between counts before and after the hurricane are indicated by *.

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THE BIRDS OF THE EXUMAS, BAHAMA ISLANDS

DONALD W. BUDEN[1]

ABSTRACT.—One hundred and twenty-five species of birds are recorded living in the Exumas, 50 for the first time; 11 others are known only as fossils. Records of 14 other species are considered questionable. Of 50 probable breeding species, 25 are land birds, including the introduced Rock Dove (*Columba livia*) and Common Peafowl (*Pavo cristata*). The Greater Flamingo (*Phoenicopterus ruber*) and Red-legged Thrush (*Turdus plumbeus*) are former breeders, and the White-winged Dove (*Zenaida asiatica*) probably has colonized recently from the southern Bahamas. Nests, eggs, and young are reported for 33 species, 22 of them for the first time in the Exumas. The Bananaquit (*Coereba flaveola*) was the most frequently encountered species during summer 1991. *Received 25 Nov. 1991, accepted 30 April 1992.*

This report is the first review of the birds of the Exumas and is based largely on my observations covering over 60 different islands during 14–19 December 1990 and 20 May–2 August 1991, together with records gleaned from the scanty literature, data from museum specimens, and unpublished reports by other observers.

STUDY AREA AND ORNITHOLOGICAL HISTORY

The Exumas comprise a chain of about 600–700 islands stretching 200 km along the eastern edge of the Great Bahama Bank (Fig. 1). They range from barren or sparsely vegetated rocks no more than a few square meters in area to predominately scrub-covered islands with patches of xeric-to-semimesic woodlands, the largest being Great Exuma. The Ministry of Education (1985) gives the combined areas of Great and Little Exuma as 186 km² (with maximum elevation 38.1 m), and that of the Exuma Cays as 104 km² (max. elev. 39.6 m). My measurements of Great Exuma (141 km²) and Little Exuma (25 km²) total slightly less. Barraterre, Madame Dau's Cay, Great Exuma, and Little Exuma are linked by causeways.

In 1980 there were 3767 residents in the Exumas (Ministry of Education 1985), most of them on Great Exuma; the Exuma Cays (islands north of Baraterre and referred to herein as the cays) are populated sparsely. Wildlife receives some protection in the Exumas Land and Sea Park, which extends from just south of Wax Cay to Rocky Dundas, but housing and other developments on private islands are sources of progressive habitat deterioration both within and outside park boundaries.

Bryant (1859) reported briefly some of his observations in the Exumas in 1859, as did Cory (1880) on his visit to the northern cays in 1879. Specimens Cory collected are in the Field Museum of Natural History (FMNH), along with six Burrowing Owls collected on Great Exuma for Cory by J. H. Ingraham in 1892. Chapman (1908) mentioned several species he saw during a brief stop at Norman's Cay on 31 March 1907.

C. J. Maynard visited the Exumas in 1883, 1884, 1893, and 1915, mainly to collect *Cerion* snails. Some of his observations on the birds are scattered among his privately published and little-known books and journals, and the 82 study skins of 19 species he collected are in the Museum of Comparative Zoology, Harvard Univ. (MCZ), eight of them from Highborne Cay on 8 and 9 April 1893, and the others from islands throughout the chain during

[1] Natural Sciences, Northern State Univ., Aberdeen, South Dakota 57401.

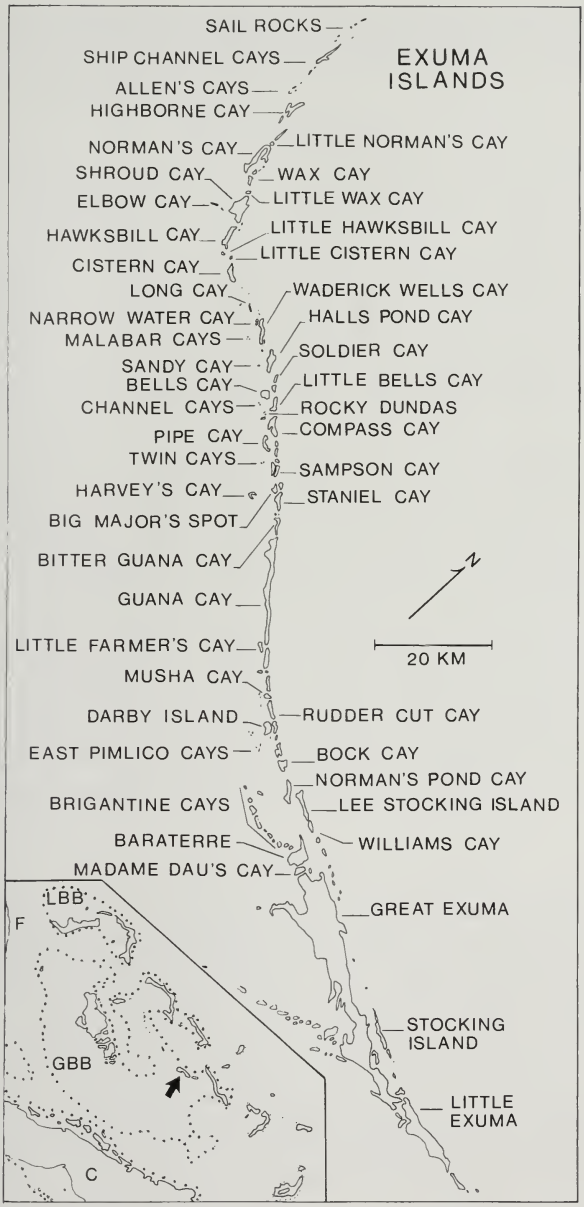

FIG. 1. Map of the Exuma Islands. Inset arrow points to Great Exuma, C = Cuba, F = Florida, GBB = Great Bahama Bank, LBB = Little Bahama Bank. Guana Cay = Great Guana Cay.

5 March–1 April 1915. The names of the islands and settlements where he collected birds in 1915 (listed geographically from north to south) and the dates are Highborne Cay, 5 March, Cistern Cay, 1 April, Conch Cut Cay (=Rocky Dundas?), 12 March, Sampson Cay, 13 March, Harvest Cay (=Harvey's Cay), 13 and 16 March, Bitter Guana Cay (visited on 14 and 31 March, but collection date of Osprey unstated), Black Point (northern end of Great Guana Cay), 14 March, Cave Cay, 17 March, Norman's Pond Cay, 19 March, Refuge Cay (=Lee Stocking Island)—see Maynard (1926:238), 20 March, Anne's Tract (settlement on Baraterre), 20 March, Great Exuma (including Roseville = Rolleville, a settlement on the northeastern coast), 20–24 March, Brigantine Cays, 28 March, Green Turtle Cay, 24 March, and Little Exuma, 23 March. Some specimens labeled as from Norman's Pond are cataloged under Norman's Cay, all of them collected on 19 March when Maynard was in the southern Exumas thus indicating the correct locality is Norman's Pond Cay.

Allen (1961a, b) mentioned some of the birds he saw in the northern Exumas (Norman's Cay southward to Waderick Wells Cay) in January 1958. Bond (1964) listed several species he saw on Great Exuma in late January 1964, and he included additional notes on Exuma birds in this and other supplements to his 1956 check-list of West Indian birds (Bond 1962, 1963, 1964, 1970, 1973, 1978, 1982, 1984). Thirteen specimens of seven species collected on Staniel Cay, Big Major's Spot, and Bitter Guana Cay by G. A. Darling, M. W. Hucks, and J. K. Lewis on 23 and 24 December 1967 were deposited in the Albert Schwartz Collection (AS) now in the Louisiana State University Museum of Natural Science.

M. H. Clench's field notes contain records of birds she saw during brief visits to Great Guana Cay on 4 March and Great Exuma on 6 March 1976, and Sprunt (1984) summarized breeding records of seabirds in the Bahamas, including his observations in the Exumas during the late 1970s and early 1980s. Additional records have been contributed by D. Lonsdale, Assistant Director of the Shedd Aquarium, who visited the northern Exumas during a cruise of the *Coral Reef* II, 16–28 April 1989, J. B. Dunham, K. Burnett, and G. Wenz, who compiled a list of the birds seen on Lee Stocking Island and the northern Great Exuma region by the staff of the Caribbean Marine Research Center during February 1987–April 1989, and R. Sutherland who listed birds seen on kayak expeditions to the northern Exumas (Allen's Cays to Staniel Cay) during March–May 1991, and some in April 1989 and 1990.

METHODS

Scientific and English names follow the American Ornithologists' Union (1983, 1989, 1991), with exceptions noted in Buden (1992). Abbreviations of frequently used names of observers and sources of records are BBL = Bird Banding Laboratory, Laurel, Maryland, DWB = Donald W. Buden, JBD et al. = J. B. Dunham, K. Burnett, and G. Wenz, PH = Peggy Hall, PR-L = Pauline Rodgers-Lee, and RS = Robert Sutherland.

Terms describing occurrence are nonbreeding visitor (mainly in passage or overwintering), resident (occurring year-round, breeding), and summer visitor (breeding). Terms describing abundance are very common (30 or more/day), common (15–30/day), fairly common (5–15/day), uncommon (1–5 on most days), scarce (5–15/season), and rare (1–5/season). Bird counts on Great Exuma were made along roads and trails covering 112 km during July 1991, the distances being estimated from Bahamas government maps (Lands and Surveys Dept. 1968–1969). I measured the areas of Great and Little Exuma by superimposing a scaled 0.2-km grid over 1:25,000 scale maps and counting the grid squares, estimating coverage in the partially filled squares.

Locality records are summarized for common, widely distributed species and annotated in greater detail for others; all breeding records are listed. Species reported as occurring

"throughout" have been recorded on both Great Exuma and Little Exuma and are widespread in the cays. Species known in the Exumas only as fossils are listed separately, and species recorded in the Exumas for the first time (including old specimen records unreported in the literature) are indicated by asterisks.

SPECIES ACCOUNTS

Least Grebe (*Tachybaptus dominicus*).—Uncommon resident on Great Exuma where recorded by Bond (1956) and where I saw several pairs during July 1991. The only record for the cays is a pair seen on Lee Stocking Island in July 1988 (JBD et al.). Breeding.—One adult flushed from an empty nest on Great Exuma, 8 July 1991 (DWB).

Pied-billed Grebe (*Podilymbus podiceps*).*—Status uncertain, possibly scarce resident. One seen off a beach on Lee Stocking Island in April 1989 (JBD et al.) and three others at three different ponds on Great Exuma on 16 July 1991 (DWB).

Audubon's Shearwater (*Puffinus lherminieri*).—Common "summer" visitor to many of the small, rocky islets, especially in the northern part of the chain. Breeding.—Ship Channel Cays, eggs, 24 March 1859 (Bryant 1859:132), and recorded nesting during the late 1800s (Maynard 1895: 39); Allen's Cays, many heard calling at night, 28 March 1991 (RS), many calling and landing disoriented on boats at night during May and June 1991 (reports from visiting yachters), ca 50 desiccated carcasses of fully grown birds presumably from 1990 breeding season, plus numerous weather-worn bones from previous seasons, all on Allen's Cay, 19 December 1990 (DWB), and Maynard's (1894) mention of "a key that lies about half a mile north of U Key [=Southwest Allen's Cay] . . . called Pimlico Key, on account of the abundance of the Pimlico or Audobon's [sic] Shearwater which inhabit it" probably is referable to Allen's Cay; Long Cay, ca 40 dead (mainly young) in a sinkhole in 1980 (PH), and several young seen and ca 500 breeding pairs roughly estimated on 29 and 30 May 1991 (D. Lee); East Pimlico Cays, ca six pairs with eggs and young in a cave during July 1990 (R. Dill). Additional sightings, but no direct evidence of breeding on Little Norman's Cay in early May 1991 (A. Potts), Little Cistern Cay on 24 April, Sandy Cay on 16 April, and Twin Cays on 15 April 1991 (RS), and on Rocky Dundas where bones were found near the mouth of a cave on 14 June 1991 (DWB).

Wilson's Storm-Petrel (*Oceanites oceanicus*).—Nonbreeding visitor. A female (FMNH 33446) was collected at Highborne Cay on 15 May 1879, presumably by the Cory expedition.

White-tailed Tropicbird (*Phaethon lepturus*).—Common summer visitor throughout the cays, but much less numerous on Great and Little Exuma and immediately adjacent islets. Early date: Shroud Cay, 26 March

1991 (RS). Breeding.—Norman's Cay, "nesting," early June 1991 (reports from visiting yachters); Shroud Cay, "nesting," 20 April 1991 (RS), ca 50 adults and many downy young seen on yearly visits in July, 1985–1989 (G. Roberts), and young in burrows on 1 August 1987 (PH); Elbow Cay, one adult in burrow, 5 June 1991 (PH); Little Hawksbill Cay, one adult in burrow, 8 June 1991 (DWB); Waderick Wells Cay, ca 20 pairs with eggs and young during 21 May–26 June 1991, and ca 50 pairs estimated total, and mainly along northeastern coast (DWB); Halls Pond Cay, "nesting," (PH); Little Bells Cay, one adult in burrow, 28 May 1991 (D. Lee); Long Rock (off western coast of Great Exuma), breeding "in holes in the horizontal surface of the rock" (Bryant 1859:128); and Sprunt (1984) reported recently confirmed breeding on Shroud Cay, Waderick Wells Cay, and Little Bells Cay.

Brown Pelican (*Pelecanus occidentalis*).*—Nonbreeding visitor. Singles seen at Waderick Wells Cay on 9 June 1991 (DWB), Ship Channel Cays, Allen's Cays, and Great Exuma during May–July 1991 (reports from visitors and local residents), and Lee Stocking Island occasionally in April (JBD et al.) and one on 19 July 1991 (L. Cain).

Double-crested Cormorant (*Phalacrocorax auritus*) and Neotropic Cormorant (*P. brasilianus*).—Cormorants are known in the Exumas only from a scattering of sight records. JBD et al. recorded one *P. brasilianus* on Lee Stocking Island in October 1987, RS recorded one at Allen's Cays on 28 March 1991, and PR-L (in Bond 1968) reported *P. auritus* on "Great and Little Exuma." However, in view of the absence of specimens or other corroborative evidence, and because of the possibility of confusing examples of the diminutive, Bahaman race of the Double-crested Cormorant with the Neotropic Cormorant (see Watson et al. 1991), the taxonomic status of cormorants in the Exumas is uncertain; to what extent one or the other or both species occur is unknown. I saw no more than 12 cormorants and no more than two together in the Exumas during summer 1991, all on Great and Little Exuma in July, and none of the islanders queried knew of any breeding locally.

Magnificent Frigatebird (*Fregata magnificens*).*—Nonbreeding visitor. Seen occasionally throughout the cays and 5–6 regularly at Barren Rocks, north of Waderick Wells Cay (PH)—four there on 3 June 1991 (DWB).

Great Blue Heron (*Ardea herodias*).*—Nonbreeding visitor. One seen on Waderick Wells Cay on 15 December and possibly the same bird on Halls Pond Cay, 16 December 1990 (DWB), recorded in the northern Exumas in January 1958 (Allen 1961b), four seen at Allen's Cays on 28 March, and one each at Bells Cay on 24 March, Shroud Cay on 20 April, and Saddle Cays (south of Cistern Cay) on 24 April 1991 (RS), and seen occasionally year-round on Lee Stocking Island (JBD et al.).

Great Egret (*Casmerodius albus*).*—Status uncertain. Three seen on

Compass Cay, 12 April 1991 (RS), one on Great Exuma on 6 March 1976 (M. H. Clench), and several others during July 1991 (DWB), and JBD et al. reported occasional summer visitors on Lee Stocking Island, and migratory flocks there and on Great Exuma in October.

Snowy Egret (*Egretta thula*).—Status uncertain. Several seen on a rock off the eastern shore of Halls Pond Cay, undated (PH), singles off Staniel Cay on 23 March and Bells Cay on 24 March 1991 (RS), and on Great Exuma on 16 July 1991 (DWB), and "occasional year-round visitors" in the Lee Stocking Island–northern Great Exuma region (JBD et al.). Recorded from "Exuma" by Bond (1956).

Little Blue Heron (*E. caerulea*).*—Status uncertain. Two seen on Shroud Cay on 20 April and two at Saddle Cays (north of Waderick Wells Cay), 24 April 1991 (RS), and two on Great Exuma, one each on 7 and 31 July 1991 (DWB).

Tricolored Heron (*E. tricolor*).*—Probably fairly common at least on Great Exuma where it was seen regularly during July 1991 (DWB). Breeding is undocumented. Singles seen on Shroud Cay, 26 April 1989 (D. Lonsdale), and 4 June 1991 (DWB), and others seen year-round in the Lee Stocking Island–northern Great Exuma region (JBD et al.).

Reddish Egret (*E. rufescens*).*—Status uncertain, possibly breeding in small numbers. One dark morph seen at Pipe Cay on 1 June 1991, and single white morphs on Great Exuma on 7 and 31 July, and on Little Exuma, 30 July 1991 (DWB), and one immature white morph on Lee Stocking Island on 15 July 1991 (L. Cain).

Cattle Egret (*Bubulcus ibis*).—Status uncertain. One seen on Highborne Cay, 16 December 1990 (DWB), a pair copulating on a boat at Waderick Wells Cay, 22 April 1991 (PH), singles and small flocks occasionally in the Lee Stocking Island-northern Great Exuma region year-round (JBD et al.), several on Great Exuma in late January 1964 (Bond 1964), and up to four together at a dump there in July 1991 (DWB).

Green-backed Heron (*Butorides virescens*).—Common resident throughout. Breeding.—Five recently fledged young together on Shroud Cay, 3 June 1991 (DWB).

Yellow-crowned Night-Heron (*Nyctanassa violacea*).—Common resident throughout. Breeding.—A nest with two eggs ca 1 m high in a small tree, Sandy Cay, 2 June 1991 (DWB).

Glossy Ibis (*Plegadis falcinellus*).—Nonbreeding visitor. One seen on Great Exuma in April and another in August, years unrecorded (B. Minns), and recorded on "Great and Little Exuma" (PR-L in Bond 1968).

Roseate Spoonbill (*Ajaia ajaja*).—Nonbreeding visitor. Recorded from "Exuma" (Bond 1956), and one seen on Lee Stocking Island in March 1988 (JBD et al.).

Fulvous Whistling-Duck (*Dendrocygna bicolor*).—Probably a non-

breeding visitor. A pair was seen on Lee Stocking Island several times in May 1987 (JBD et al.), and Bond (1964) reported that B. Minns saw ca 75 together on Great Exuma and shot two, one of which was examined by R. D. Wood in late February 1964.

West Indian Whistling-Duck (*D. arborea*).*—Resident and probably more numerous than records indicate, at least on the southernmost islands. C. Clark of Moss Town, Great Exuma reported (pers. comm.) small flocks of 2–5 seen regularly at Coakley Cay, Culmers Cay, and Jewfish (=Hummingbird) Cay, all off the western coast of Great Exuma, and many other local residents consider it an agricultural pest on Great and Little Exuma, but more numerous in the past when farming was more widespread. I saw only two on Great Exuma (one on 7 July, another on 2 August), two on Lee Stocking Island on 30 June, and one on Bock Cay on 3 July 1991. Two others were seen at Waderick Wells Cay in April 1989, 6–10 in the vicinity of Pipe Cay in April 1990, and one on Shroud Cay on 6 April 1991 (RS), and another at Waderick Wells Cay on 21 April 1988 (crew of the yacht *Azimuth*). Breeding.—A pair of adults with 11 ducklings on Lee Stocking Island in September 1988, three of the young still present in December 1988 (JBD et al.).

White-cheeked Pintail (*Anas bahamensis*).*—A fairly common resident on Great Exuma where small groups of 5–20 were seen regularly during July 1991 (DWB), but less numerous in the cays. The absence of records from Little Exuma is probably artifactual. Five were seen on Waderick Wells Cay on 9 June 1991 (DWB), one on Halls Pond Cay in July 1990 (L. Roth), and others on Lee Stocking Island during spring and early summer 1988 (JBD et al.). The only winter records are 15 at a pond on Narrow Water Cay in January 1988 (PH). Breeding.—One adult with several flightless young swimming in the anchorage off the northern end of Waderick Wells Cay, date unrecorded (PH).

Northern Pintail (*A. acuta*).—Nonbreeding visitor. A female banded in Maryland on 19 January 1967 was shot at Great Exuma in October 1967 (Buden 1991, BBL files).

Blue-winged Teal (*A. discors*).—Nonbreeding visitor. Fifteen seen at a pond on Waderick Wells Cay, 26 February 1989 (PH), and 15 banded in Canada and the United States, 1948–1973, were shot during October–March 1945–1975, 13 of them at Great Exuma, two at Little Exuma, and one between Great Guana Cay and Darby Island (Buden 1991, BBL files).

Northern Shoveler (*A. clypeata*).*—Nonbreeding visitor. A flock of 40–50 seen on Great Exuma during November 1989–January 1990 (M. Minns).

American Wigeon (*A. americana*).—Nonbreeding visitor. A female banded in Manitoba on 23 September 1952 was recovered at Great Exuma

in February 1954, and a male banded in New York on 6 October 1953 and another in Saskatchewan on 11 July 1957 were shot at Little Exuma on 15 March 1959 and in December 1957, respectively (Buden 1991, BBL files).

Ring-necked Duck (*Aythya collaris*).—Nonbreeding visitor. A male banded in Ohio on 22 March 1961 was shot at Great Exuma on 20 February 1964 (Buden 1991, BBL files).

Red-breasted Merganser (*Mergus serrator*).*—Nonbreeding visitor. A female with a broken leg on Lee Stocking Island in November 1987 was hand fed fish daily for about a month before it recovered and flew away on 18 December, and was last seen in the area on 25 December 1987 (JBD et al.).

Ruddy Duck (*Oxyura jamaicensis*).—Status uncertain, possibly breeding. Not uncommon on Great Exuma in winter (M. Minns), but the only breeding record for "Great and Little Exuma" (PR-L in Bond 1968) requires confirmation.

Osprey (*Pandion haliaetus*).—Fairly common resident in the cays, but scarce on Great and Little Exuma. Breeding.—Nests seen on an islet off Highborne Cay, on Norman's Cay (2), Little Hawksbill Cay, Hawkfish Rocks (north of Waderick Wells Cay), Sandy Cay, Rudder Cut Cay, and Lee Stocking Island, all during 1987–1991 (DWB and others); a set of three eggs collected in the "Exuma Cays," 5 March 1949 (Wolfe 1951, Bond 1952), and another set the first week of November 1951 (Bond 1952).

Northern Harrier (*Circus cyaneus*).—Nonbreeding visitor. Recorded on "Great and Little Exuma" (PR-L in Bond 1968), and one seen on Lee Stocking Island, 23 April 1989, and another on Barraterre in October 1989 (JBD et al.).

American Kestrel (*Falco sparverius*).—Uncommon resident on Great Exuma where seen year-round (JBD et al.) and where several pairs were observed in July 1991 (DWB), and recorded on "Great and Little Exuma" by PR-L (in Bond 1968). But no records from the cays north of Lee Stocking Island. One female perched atop a telephone pole on Little Exuma on 30 July 1991 had a pronouncedly streaked breast and may have been a migrant, whereas all others I saw at close range had a white, unstreaked (or nearly so) breast characteristic of the resident "Cuban subspecies," *F. s. sparveroides.*

Merlin (*F. columbarius*).—Nonbreeding visitor. One seen on Highborne Cay, 17 December 1990, another on Waderick Wells Cay, 22 May 1991 (DWB), and one each on Compass, Hawksbill, Little Cistern, and Wax cays on 2, 9, 18, and 22 April 1991, respectively (RS). A female was

collected on Sampson Cay by C. J. Maynard on 13 March 1915, and a female banded in New Jersey on 8 October 1979 was recovered at Little Exuma on 10 December 1979 (Buden 1991, BBL files).

Peregrine Falcon (*F. peregrinus*).—Nonbreeding visitor. A dead bird was found at Norman's Pond Cay, date unrecorded (Bryant 1859:105), one was "killed" at Norman's Cay on 7 January 1879 (Cory 1880:129), another was seen at Allen's Cays on 19 December 1990 (DWB), and several others between Allen's Cays and Rocky Dundas during 24 March–25 April 1991 (RS).

Common Peafowl (*Pavo cristatus*).*—Introduced on Great Exuma during the 1950s by J. L. Riggs (B. Minns, pers. comm.), and well-established island-wide, but secretive and more often heard than seen. Breeding.—A female with two chicks seen southwest of Georgetown, 27 July 1991 (DWB).

Clapper Rail (*Rallus longirostris*).—Common resident throughout but breeding is undocumented.

Purple Gallinule (*Porphyrula martinica*).*—Nonbreeding visitor. One found dead in the road at Hartswell, Great Exuma in early 1991 (M. Minns).

Common Moorhen (*Gallinula chloropus*).*—Probably resident at marshes and ponds throughout, but unrecorded on Little Exuma. Seen occasionally at Waderick Wells Cay in May and June 1991, and regularly (maximum three together) on Great Exuma in July 1991 (DWB). One was found dead at Lee Stocking Island on 14 March 1989 and another was seen on Great Exuma, 29 April 1989 (JBD et al.). Breeding.—Two adults with young at Little Wax Cay on 23 June 1988 (PH), and one adult on a nest with four eggs at a freshwater pond on Great Exuma, 15 July 1991 (DWB).

American Coot (*Fulica americana*).—Nonbreeding visitor. Local hunters consider "coots" common on Great and Little Exuma in winter. Five banded in Manitoba, Illinois (2), Minnesota, and New Jersey during 1945–1966 were shot at Great Exuma (4) and Little Exuma (1), two of them in November, one each in January and February, and one undated, and another banded in Louisiana on 27 November 1937 was shot between Darby Island and Great Exuma on 18 November 1938 (Buden 1991, BBL files).

Black-bellied Plover (*Pluvialis squatarola*).—Nonbreeding visitor. Recorded throughout the cays and on Great and Little Exuma, being more numerous in winter than summer.

Snowy Plover (*Charadrius alexandrinus*).—Status uncertain. Recorded in the northern Exumas in January 1958 (Allen 1961b), on Great Exuma in late February 1964 (R. D. Wood in Bond 1964), and on "Great and

Little Exuma" during 1966–1968 (PR-L in Bond 1968), none of the accounts mentioning numbers observed.

Wilson's Plover (*C. wilsonia*).—Common summer visitor throughout; possibly resident in small numbers. I saw none during a week on Allen's, Highborne, Waderick Wells, and Halls Pond cays in December 1990, but JBD et al. recorded it year-round on Lee Stocking Island. C. J. Maynard collected specimens on Harvey's Cay, Great Guana Cay, Farmer's (=Little Farmer's) Cay, Norman's Pond Cay, Great Exuma, and the Brigantine Cays during 14–28 March 1915, and JBD et al. reported a flock of over 200 on a small cay near Baraterre in September 1958. Breeding (all records are 1991 and from sandy beaches).—A clutch of three eggs on Great Guana Cay on 28 June (PH, DWB), another of two eggs on Norman's Pond Cay in early June and one egg on Lee Stocking Island in mid-June (L. Cain), and one adult with three recently fledged young on Great Exuma on 7 July, and another adult with two flightless young on Little Exuma, 30 July (DWB).

Semipalmated Plover (*C. semipalmatus*).*—Nonbreeding visitor. Singles seen at Waderick Wells Cay on 22 May, Pipe Cay on 1 June, and Little Exuma on 26 July 1991 (DWB).

Killdeer (*C. vociferus*).—Probably an uncommon to fairly common resident, at least on Great and Little Exuma; seen occasionally in the cays, but no summer records. Breeding is undocumented. Summer birds almost certainly are the West Indian subspecies, *C. v. ternominatus,* whereas the winter population probably includes both *C. v. ternominatus* and migrant *C. v. vociferus* from Canada and the United States, one example of which was collected on Norman's Cay by C. B. Cory on 7 January 1879 (FMNH 36514, female, wing length 172 mm).

American Oystercatcher (*Haematopus palliatus*).—Uncommon resident throughout; at least one or two pairs were seen on most of the larger cays visited during summer 1991 (DWB). Breeding is undocumented.

Black-necked Stilt (*Himantopus mexicanus*).—Common summer visitor at shallow ponds throughout. No winter records. Breeding.—"Nesting" on Norman's Cay (PH), and three flightless young seen at Rolletown Pond, Great Exuma on 8 July 1991 (DWB).

Greater Flamingo (*Phoenicopterus ruber*).—Former breeder, currently nonbreeding visitor. Allen (1956:122, 127) reported a nesting site at "Norman's Pond" deserted probably during the 1870s, his information based on a letter from L. E. W. Forsyth dated 21 March 1954. This locality doubtless is Norman's Pond Cay as indicated in Allen's (1956:69) map of Caribbean breeding sites, and not Norman's Cay as indicated in his map detailing northern Bahama breeding colonies (Allen 1956:189). The only other records for the Exumas are 19 immatures I saw feeding at Blue

Pond, near Rocker's Point, Great Exuma on 29 July 1991, possibly visitors from Great Inagua. Several residents of Great Exuma recalled seeing flamingos from time to time, but none was aware of any breeding there.

Greater Yellowlegs (*Tringa melanoleuca*).—Nonbreeding visitor. Recorded throughout from 7 July (Great Exuma, 1991, DWB) to 9 April (Hawksbill Cay, 1991, RS)—maximum 9 together, Great Exuma, 31 July (DWB).

Lesser Yellowlegs (*T. flavipes*).—Nonbreeding visitor. Ca 15 seen on Halls Pond Cay on 15 December 1990 (DWB), two at Harvey's Cay, 12 March 1915 (Maynard 1920), and several on Great and Little Exuma during July 1991 (DWB).

Willet (*Catoptrophorus semipalmatus*).*—Fairly common throughout in summer; possibly resident, but no winter records. Breeding is undocumented, but many territorial pairs were seen during May–July 1991 (DWB).

Spotted Sandpiper (*Actitis macularia*).—Nonbreeding visitor. Recorded in small numbers throughout from 18 July (Great Exuma, 1991, DWB) to 25 April (Pipe Cay, 1991, RS).

Upland Sandpiper (*Bartramia longicauda*).—Nonbreeding visitor. One seen on Bitter Guana Cay, 31 March 1915 (Maynard 1920).

Ruddy Turnstone (*Arenaria interpres*).*—Nonbreeding visitor. Recorded throughout and year-round, but less common in summer than winter.

Sanderling (*Calidris alba*).*—Nonbreeding visitor. Two seen in the Pipe Cay area, two on Sandy Cay, and nine on Hawksbill Cay during 15–22 April 1991 (RS), two on Halls Pond Cay, 25 April 1989 (D. Lonsdale), and seven on Shroud Cay on 4 June, and three on Hawksbill Cay on 7 June 1991 (DWB).

Semipalmated Sandpiper (*C. pusilla*).—Nonbreeding visitor. A "few" seen at Harvey's Cay on 12 March 1915 (Maynard 1920). No other records, but probably present among the many unidentified sandpipers I saw on Great and Little Exuma in July 1991.

Least Sandpiper (*C. minutilla*).*—Nonbreeding visitor. Up to 11 together on Great Exuma occasionally during the last two weeks of July 1991 (DWB), and "flocks" seen occasionally on Lee Stocking Island and Great Exuma during spring and fall 1988 (JBD et al.).

Short-billed Dowitcher (*Limnodromus griseus*).—Nonbreeding visitor. Recorded on "Great and Little Exuma" (PR-L in Bond 1968), and dowitchers (probably *L. griseus*) have been recorded in the northern Exumas during 19–28 January 1958 (Allen 1961b) and on Halls Pond Cay on 25 April 1989 (D. Lonsdale).

Parasitic Jaeger (*Stercorarius parasiticus*).*—Nonbreeding visitor. One was seen near the Brigantine Cays in February 1988 (JBD et al.).

Laughing Gull (*Larus atricilla*).—Common summer visitor throughout. Breeding.—One hundred and fifty pairs "courting and building nests," Sail Rocks, May 1981 (Sprunt 1984); several pairs and one clutch with two eggs and another with one egg and one nestling on an islet off the southeastern tip of Shroud Cay, 3 June 1981 (DWB); and one large chick in a colony of several pairs on the Malabar Cays, 22 June 1991 (DWB).

Herring Gull (*L. argentatus*).*—Nonbreeding visitor. One seen daily in the harbor at Highborne Cay, 16–18 December 1990 (DWB).

Gull-billed Tern (*Sterna nilotica*).*—Uncommon summer visitor to some of the larger cays, and fairly common on Great and Little Exuma where I saw small groups of 2–15 regularly during July 1991. No direct evidence of breeding, but many immatures I saw on Great Exuma in July probably were hatched there.

Royal Tern (*S. maxima*).*—Uncommon summer visitor throughout. RS recorded up to ten together on at least 12 different islands from Norman's Cay to Staniel Cay during 24 March–25 April 1991, but the only mid-winter record is one I saw on a channel marker at the tip of Norman's Spit (off Norman's Cay), 16 December 1990. One banded as a flightless young in Virginia on 14 July 1966 was recovered at Great Exuma on 11 July 1967 (Buden 1991, BBL files). Breeding.—Colony, 27 single-egg clutches on an islet off the northeastern tip of Hawksbill Cay, 3 June 1991 (DWB).

Sandwich Tern (*S. sandvicensis*).*—Uncommon summer visitor among the cays; unrecorded from Great and Little Exuma. Breeding.—Several nesting pairs and two single-egg clutches at Lightning Rocks (off Long Cay) on 29 May 1991, and a colony of ca 30 adults with 13 single-egg clutches on an islet off the northeastern tip of Hawksbill Cay, 3 June 1991 (DWB).

Roseate Tern (*S. dougallii*).—Fairly common summer visitor among the cays, but scarce on Great and Little Exuma. Breeding.—A pair with one egg at Lightning Rocks on 29 May, ca 30 adults and ten single-egg clutches on an islet off the eastern coast of Halls Pond Cay on 1 June [16 abandoned eggs and no adults during revisit, 25 June], ca 25 adults and two clutches (one with one egg, the other with two) on an islet off the southern tip of Waderick Wells Cay, 9 June, and ca 150 adults with many chicks and eggs at Channel Cays, 14 June 1991 (DWB), and nesting confirmed on Hawksbill Rock (off Hawksbill Cay?) and Little Bells Cay (Sprunt 1984).

Least Tern (*S. albifrons*).—Common summer visitor throughout.

Breeding.—Two colonies, ca five and three pairs, both with two-egg (mainly) and single-egg clutches, Waderick Wells Cay, 21–27 May 1991 (DWB); ca ten adults and two two-egg clutches on an islet off the eastern coast of Halls Pond Cay, 1 June 1991 [eight abandoned eggs and no adults when revisited on 25 June] (DWB); ca 20–30 adults and many eggs on Elbow Cay, 5 June 1991 (PH); colony, 15 clutches (five with one egg, five with two eggs, four with one chick, and one with one chick and one egg), an islet off the southern tip of Waderick Wells Cay, 9 June 1991 (DWB); and recorded nesting on Little Bells Cay (Sprunt 1984).

Bridled Tern (*S. anaethetus*).—Summer visitor and probably more numerous than records indicate as some may go undetected among large flocks of Sooty Terns. I saw 10–15 on the Malabar Cays on 22 June and as many at Channel Cays on 25 June, but none elsewhere during summer 1991. Breeding.—Eggs "in an advanced state of incubation" at Ship Channel Cays in late May [1884?] (Maynard 1895:43), and one egg at Channel Cays on 25 June 1991 (DWB).

Sooty Tern (*S. fuscata*).—Common summer visitor and probably occurring on small, uninhabited islands throughout the chain, but no records south of Channel Cays. Breeding.—Colony, single-egg clutches "in an advanced state of incubation" on Ship Channel Cays on 8 and 9 June [1884?] (Maynard 1895:43); colonies (ca 20–40 pairs each, 200–300 pairs total) on islets between Cistern Cay and Waderick Wells Cay (including Saddle Cay mentioned by Sprunt [1984]), with eggs first seen on 29 May and young beginning 11 June 1991 (DWB) (some of the colonies numbering over 100 pairs each in recent years [PH]); 75–100 pairs and many eggs on Sandy Cay on 2 June, and 30–40 pairs and several eggs at Channel Cays on 14 June 1991 (DWB); and one banded as a recently fledged young in the Dry Tortugas, Florida on 13 June 1965 was recovered at a nest in the northern Exumas on 28 June 1972 (Buden 1991, BBL files).

Brown Noddy (*Anous stolidus*).—Common summer visitor and probably occurring on small uninhabited islands throughout the chain, but unrecorded south of Staniel Cay. Breeding.—"Hundreds" nesting on Little Norman's Cay in late May 1991 (A. Potts); colonies (ca 5–40 pairs each, 150–250 pairs total) on islets between Cistern Cay and Waderick Wells Cay (including Saddle Cay mentioned by Sprunt [1984]), with many eggs during late May to mid-June 1991 (DWB) (some of the colonies numbering over 100 pairs in recent years [PH]); and several pairs each on Rocky Dundas and on islets off Staniel Cay and Pipe Cay on 31 May and 1 June 1991 (DWB).

Rock Dove (*Columba livia*).*—Introduced and recorded only in settlements on Great Exuma. Two seen in Georgetown on 6 March 1976 (MHC) are the first records. Common in Georgetown, 15 seen at Farmer's Hill, and six others at The Forest, all in July 1991 (DWB).

White-crowned Pigeon (*C. leucocephala*).—Common to very common resident throughout and more numerous in summer than winter. Up to 1500 together on a small cay off the western coast of Great Exuma during one recent fall (M. Minns). Breeding.—A nest with two eggs, Little Bells Cay, 28 May 1991 (DWB); colony, ca 20 pairs, four nests with two eggs and one with one egg, Waderick Wells Cay, 29 May 1991 [ca 100 pairs estimated islandwide] (DWB); three nests each with two eggs and one with two nestlings on Sandy Cay on 2 June, two others with two eggs on Shroud Cay on 4 June, and another with one pin-feathered young on Rocky Dundas, 14 June 1991 (DWB); and nesting on Long Rock (off the western coast of Great Exuma), date unrecorded (Bryant 1859:120).

White-winged Dove (*Zenaida asiatica*).*—Probably a scarce and recently established resident on Great Exuma, where seen occasionally in ones and twos during July 1991 (DWB). M. Minns, who has hunted birds on Great Exuma for many years had not seen any prior to summer 1991, but he told me other hunters began seeing them on nearby Long Island during the mid-1980s, first at the southern end and more recently islandwide. Those I saw on Long Island during summer 1990, including one incubating, were reported as first records (Buden 1992).

Zenaida Dove (*Z. aurita*).*—Fairly common resident throughout the cays (maximum 15 together on Lee Stocking Island, 2 July, 1991, DWB), but uncommon on Great and Little Exuma. Breeding.—Two eggs in a shallow, sandy depression sparsely lined with grasses in a patch of sea oats (*Uniola*) on Waderick Wells Cay, 21 May 1991 (DWB).

Mourning Dove (*Z. macroura*).—Uncommon resident on Great and Little Exuma, but unrecorded in the cays north of Baraterre. Known on Little Exuma at least since the 1930s (Bond 1936:150), but more numerous since the introduction of birds from Nassau to Georgetown, Great Exuma by N. Minns in the early 1980s.

Common Ground-Dove (*Columbina passerina*).—Common to very common resident throughout. Breeding.—A nest with two young, 26 May 1991 (DWB) [local residents report the nest hosted two successive broods as it contained two young on 28 April, was empty on 12 May, and contained two newly hatched young on 23 May]; two nests on Lee Stocking Island, one with two eggs in June 1987 (JBD et al.), and the other with two eggs on 2 July 1991 (DWB).

Key West Quail-Dove (*Geotrygon chrysia*).—Rare resident. One was seen on Highborne Cay on 18 December 1990 and another south of The Forest, Great Exuma on 22 July 1991 (DWB). Fossils are known from Little Exuma (Olson and Hilgartner 1982).

Mangrove Cuckoo (*Coccyzus minor*).—Fairly common resident on Great and Little Exuma, but apparently rare or scarce in the cays. More common in summer than in winter, at least on Great Exuma (M. Minns). I saw

and heard up to 13 per day from Baraterre southward to Little Exuma during 2 July–2 August 1991, but none elsewhere during 14–19 December 1990 and 20 May–2 July 1991. JBD et al. considered it fairly common in the Lee Stocking Island-northern Great Exuma region, and there are unconfirmed records from several islands in the northern part of the chain.

Yellow-billed Cuckoo (*C. americanus*).—Nonbreeding visitor. Seen in the Lee Stocking Island-northern Great Exuma region in October and in winter (JBD et al.), and recorded from "Exuma" (Bond 1956).

Smooth-billed Ani (*Crotophaga ani*).*—Fairly common resident on Great and Little Exuma, but scarce in the cays north of Baraterre where the only records are one seen at Halls Pond Cay on 15 December and seven at Highborne Cay, 17 December 1990 (DWB), one on Lee Stocking Island in June 1987 (JBD et al.), and others at Staniel Cay (J. Mann). Breeding.—Young observed on Great Exuma in late summer and early fall 1988 (JBD et al.).

Barn Owl (*Tyto alba*).—Probably a rare resident throughout the chain, but records are scanty and breeding is undocumented. I found one wing feather on Allen's Cay on 19 December 1990 and received reports from visiting boaters of a Barn Owl carrying prey on Waderick Wells Cay on 29 May 1991, and of a "large, white owl" found dead at Ship Channel Cays in early June 1991. Bond (1956) recorded *T. alba* from "Exuma" without further comment.

Burrowing Owl (*Speotyto cunicularia*).—A scarce resident throughout. I saw one on Halls Pond Cay on 16 December 1990 and another south of The Forest, Great Exuma on 22 July 1991, both during midday. I also received reports of Burrowing Owls on Norman's Cay (local police), Waderick Wells Cay (PH, B. Rader), and Bells Cay (local caretaker). Additionally, JBD et al. reported one seen on Lee Stocking Island in January 1988 and others on Great Exuma during early morning and late evening year-round, and many residents of Great Exuma told me of seeing Burrowing Owls from time to time, but less frequently in recent years. J. H. Ingraham collected 2 male, 2 female, and one unidentified as to sex, all on Exuma (=Great Exuma)—on 10 June 1892 (FMNH, originally in Cory collection). Fossils are known from Little Exuma (Olson and Hilgartner 1982).

Antillean Nighthawk (*Chordeiles gundlachii*).*—Common summer visitor throughout. Breeding.—Seventeen single-egg clutches, Waderick Wells Cay (two on 27 May, one on 13 June), Shroud Cay (three, 3–4 June), Hawksbill Cay (four, 5–6 June), Norman's Cay (one, 1 July), Bock Cay (one, 3 July), Stocking Island (one, 5 July), and Great Exuma (four, 7 July–1 August), plus several chicks and recently fledged young on Great and Little Exuma during 7 July–1 August, all 1991 (DWB); nesting on

Little Hawksbill Cay in early June, year unrecorded (PH); and one egg on Williams Cay, mid-May 1991 (A. Stoner).

Chuck-will's-widow (*Caprimulgus carolinensis*).*—Nonbreeding visitor. Heard calling at Waderick Wells Cay regularly during 22 May–27 June, and a pair flushed twice from the same buttonwood (*Conocarpus*) swamp on 12 and 26 June 1991 (DWB); recorded on Waderick Wells Cay on 24 March, 10 April, and 24 April, and on Hawksbill Cay on 9 April 1991 (RS), and heard calling at Allen's Cays on 18 June 1991 (R. Every). The Chuck-will's-widow generally is considered a rare to uncommon winter visitor to the Bahamas (Brudenell-Bruce 1975, Buden 1987a). Paterson's (1972) record of one incubating an egg on Andros Island (a first for the West Indies) during 13–26 June 1970 was accepted by the A.O.U. (1983), but not by Bond (1973:3, 1984:20), who believed it a misidentified Antillean Nighthawk. Although the recent June records lend indirect support to Paterson's claim of breeding, I consider it to be a nonbreeding visitor throughout the West Indies pending more substantial corroborative evidence to the contrary.

Bahama Woodstar (*Calliphlox evelynae*).—Uncommon to locally common resident throughout. Breeding.—Eggs and young observed in a nest on Staniel Cay during late April–early May 1990 (J. Mann), and nesting on Norman's Cay on 21 April 1991 (RS).

Belted Kingfisher (*Ceryle alcyon*).*—Nonbreeding visitor. Singles seen at Shroud Cay on 9 and 20 April and Halls Pond Cay on 17 April 1991 (RS), and others year-round in the Lee Stocking Island-northern Great Exuma region (JBD et al.).

Yellow-bellied Sapsucker (*Sphyrapicus varius*).*—Nonbreeding visitor. One undated record for Staniel Cay (J. Mann), but many unconfirmed winter records of woodpeckers throughout the Exumas doubtless pertain to *S. varius,* the only species of woodpecker occurring now, although fossils of the West Indian Woodpecker, *Melanerpes superciliaris* are known from Little Exuma (Olson and Hilgartner 1982). Additionally, the ubiquitous drill holes in tree trunks attest to the occurrence of *S. varius* throughout the region.

Eastern Wood-Pewee (*Contopus virens*).—Nonbreeding visitor. Recorded from "Great and Little Exuma" (PR-L in Bond 1968), and one collected (MCZ 332851) on Great Exuma, 24 July 1991 (DWB).

La Sagra's Flycatcher (*Myiarchus sagrae*).*—The one I saw near Moss Town, Great Exuma on 12 July 1991 is the only record and probably a vagrant from elsewhere in the Bahamas or Cuba. The nearest breeding population is on Eleuthera, 115 km north of Great Exuma and 50 km east of the northern cays.

Eastern Kingbird (*Tyrannus tyrannus*).—Nonbreeding visitor. Recorded on "Great and Little Exuma" (PR-L in Bond 1968).

Gray Kingbird (*T. dominicensis*).—Fairly common summer visitor throughout the chain, being most numerous on Great and Little Exuma. Breeding.—A nest with three young on Lee Stocking Island on 5 July, and another with an adult (incubating?) on Great Exuma on 7 July 1991 (DWB), and a pair nesting in the same palm tree on Lee Stocking Island in 1987 and 1988, the young fledging in August (JBD et al.).

Purple Martin (*Progne subis*).*—Nonbreeding visitor. One seen at Waderick Wells Cay, 19 February 1989 (PH).

Barn Swallow (*Hirundo rustica*).*—Nonbreeding visitor. Up to 11 together (but mainly ones and twos) at Norman's, Shroud, Little Cistern, Waderick Wells, Halls Pond, Compass, Twin, and Staniel cays during 1–26 April 1991 (RS), ones and twos seen occasionally at Waderick Wells Cay and Halls Pond Cay on 21 and 22 May 1991 (DWB), and small flocks in the Lee Stocking Island-northern Great Exuma region in spring (JBD et al.).

House Wren (*Troglodytes aedon*).—Nonbreeding visitor. Seen on Great Exuma in late February 1964 (R. D. Wood in Bond 1964:10).

Wood Thrush (*Hylocichla mustelina*).*—Nonbreeding visitor. One seen on Wax Cay, 22 April 1991 (RS).

Red-legged Thrush (*Turdus plumbeus*).—Probably resident during the Pleistocene when Exuma land area was greater and woodlands more extensive. The only definite record is a fossil humerus from Little Exuma (Olson and Hilgartner 1982). However, Allen (1961a:157) wrote "I landed with a party of naturalists one morning in late January [1958] on Warderick Wells. As we went ashore . . . we were immediately greeted by the loud *wet-wet* of the red-legged thrush . . . ," and in a report submitted to the Bahamas Government he (Allen 1961b) stated "Landing on the edge of a wide sandy area on the west side, we were immediately greeted by the notes of the red-legged thrush (*Mimocichla plumbea*). . . ." Neither account mentions a sighting, but Bond (1962:9) referred to Allen's "sight record" of *T. plumbeus* on Waderick Wells Cay and the Exuma Cays have since generally been considered part of its present-day range (Brudenell-Bruce 1975, A.O.U. 1983). I consider Allen's record questionable, as did Bond (1984:10, 1988:174) in some of his later publications. If indeed, Allen encountered *T. plumbeus* in the cays I believe it more likely a vagrant than a local breeding bird. *T. plumbeus* is resident in woodlands in the northern Bahamas on Grand Bahama, the Abacos, Andros, New Providence, and Cat Island, and it occurs also in the Greater and Lesser Antilles. I saw none during nearly three months in the Exumas, being based at

Waderick Wells Cay from 20 May to 27 June 1991, and none has been recorded by P. Hall, resident park warden in the northern cays since 1985.

Gray Catbird (*Dumetella carolinensis*).—Nonbreeding visitor. One seen at Halls Pond Cay on 16 December 1990 (DWB), another at Norman's Cay on 31 March 1907 (Chapman 1908:202), and two at Hawksbill Cay on 25 March 1991 (RS).

Northern Mockingbird (*Mimus polyglottos*).—Uncommon to common resident from Baraterre southward to Little Exuma, being most numerous in the settlements, and common on Norman's Cay and Staniel Cay (DWB), but unrecorded elsewhere except as an "occasional visitor" to Lee Stocking Island (JBD et al.). Breeding.—A nest with three downy young on Staniel Cay, 20 June 1991 (DWB), and two recently fledged young on Great Exuma, one on 29 April 1989 (JBD et al.), the other on 7 July 1991 (DWB).

Bahama Mockingbird (*M. gundlachii*).—Very common resident on many of the cays and on Great and Little Exuma, occurring even on small, sparsely vegetated islets and frequently seen in flight between cays. But unexpectedly absent or scarce on other seemingly suitable islands. I saw only one on Hawksbill Cay during 5–7 June 1991 and none on Shroud Cay (3–4 June), Bells Cay (26 May, 15–17 June), and Great Guana Cay (28 June), although M. H. Clench recorded two on Great Guana on 4 March 1976. Breeding (all records are 1991 DWB).—Four nests under construction (Halls Pond Cay on 23 May, Waderick Wells Cay on 20 June, and Great Exuma on 16 July and 1 August); one adult in a nest on Little Exuma, 26 July; a nest with three eggs on Rudder Cut Cay, 29 June; two recently fledged young soliciting food from an adult on Waderick Wells Cay on 18 June, and two other recently fledged young on Great Exuma, one on 20 July, the other on 1 August. The nest at Rudder Cut Cay was on the ground at the base of a clump of grass on a disused airstrip, and the five others were 0.5–5.5 m high in trees and shrubs.

Pearly-eyed Thrasher (*Margarops fuscatus*).—Nonbreeding visitor. The only record is one seen on Great Exuma in February 1964 (R. D. Wood in Bond 1964). *M. fuscatus* breeds in the Bahamas as far north as Rum Cay and San Salvador but has been recorded occasionally further north on Great Bank and Little Bank islands (Buden 1987b, 1992). Fossils from Little Exuma identified as *M. fuscatus* by Wetmore have been reidentified as *Sturnella sp.* by Olson and Hilgartner (1982).

Thick-billed Vireo (*Vireo crassirostris*).—Very common resident throughout. Breeding.—A nest with two eggs on Hawksbill Cay on 4 June and another with two eggs on Stocking Island, 17 July 1991 (DWB).

Black-whiskered Vireo (*V. altiloquus*).*—Fairly common summer vis-

itor on Great and Little Exuma, but uncommon in the cays. Seen and heard calling at Norman's, Hawksbill, Halls Pond, Bells, Staniel, and Norman's Pond cays occasionally during 23 May–1 July 1991 (DWB), and one male (MCZ 68447) was collected at Conch Cut Cay (=Rocky Dundas?) by C. J. Maynard on 12 March 1915.

Northern Parula (*Parula americana*).*—Nonbreeding visitor. Seen in the Lee Stocking Island–northern Great Exuma region occasionally in spring and fall (JBD et al.).

Yellow Warbler (*Dendroica petechia*).—Uncommon resident in mangroves throughout. Seen and heard calling on Shroud, Hawksbill, Waderick Wells, Halls Pond, and Staniel cays, and on Great and Little Exuma during 26 May–26 July 1991 (DWB), and recorded from "Exuma Cays" by Cory (1892). A male (AS 7639) and female (AS 7640) *D. p. gundlachii* were collected on Staniel Cay by J. K. Lewis on 24 December 1964.

Magnolia Warbler (*D. magnolia*).—Nonbreeding visitor. Seen on Little Wax Cay on 23 April 1989 (D. Lonsdale), Great Exuma in late January 1964 (Bond 1964), and in the Lee Stocking Island–northern Great Exuma region occasionally in fall and winter (JBD et al.).

Cape May Warbler (*D. tigrina*).*—Nonbreeding visitor. Singles seen at Norman's, Hawksbill, Waderick Wells, and Halls Pond cays during 17 April–25 May 1991, and 25 on Wax Cay on 22 April 1991 (RS), one at Halls Pond Cay on 25 April 1989 (D. Lonsdale), and one with an injured but functional wing on Waderick Wells Cay on 9 and 11 June 1991 (DWB). Recorded in the Lee Stocking Island–northern Great Exuma region during spring and fall and less frequently in winter (JBD et al.).

Black-throated Blue Warbler (*D. caerulescens*).*—Nonbreeding visitor. Two seen on Norman's Cay, 21 April, ten on Wax Cay, 22 April, and one at Halls Pond Cay, 25 April 1991 (RS). Recorded on Wax Cay also on 23 April 1989 (D. Lonsdale), and seen occasionally in the Lee Stocking Island–Great Exuma region during fall migration (JBD et al.).

Yellow-rumped Warbler (*D. coronata*).*—Nonbreeding visitor. One seen on Highborne Cay on 17 December 1990 (DWB), and three (AS 7643, 7645, 7646) collected at Big Major's Spot on 24 December 1967.

Yellow-throated Warbler (*D. dominica*).*—Nonbreeding visitor. Seen on Little Wax Cay on 23 April 1989 (D. Lonsdale) and in the Lee Stocking Island–northern Great Exuma region occasionally in fall (JBD et al.). C. J. Maynard collected one *D. d. dominica* on Harvey's Cay (MCZ 68573, 13 March 1915) and another on Great Exuma (MCZ 68573, 21 March 1915).

Prairie Warbler (*D. discolor*).—Nonbreeding visitor. Three seen on Waderick Wells Cay, 15 December, and several on Highborne Cay, 17–

18 December 1990 (DWB), and recorded from "Exuma Cays" by Riley (1905).

Palm Warbler (*D. palmarum*).—Nonbreeding visitor. Many recent winter records throughout the cays, and recorded from "Exuma Cays" by Riley (1905). The absence of records from Great and Little Exuma doubtless is artifactual.

Blackpoll Warbler (*D. striata*).*—Nonbreeding visitor. Two seen on Norman's Cay on 21 April and two others on Wax Cay, 22 April 1991 (RS).

Black-and-white Warbler (*Mniotilta varia*).*—Nonbreeding visitor. One seen on Highborne Cay on 18 December 1990 (DWB), one or two each on Norman's, Wax, Hawksbill, and Sandy cays during 17–22 April 1991 (RS), and others in the Lee Stocking Island–northern Great Exuma region occasionally in spring and fall (JBD et al.).

American Redstart (*Setophaga ruticilla*).*—Nonbreeding visitor. Recorded in ones and twos on Highborne, Norman's, Wax, and Halls Pond cays during December–May (DWB, M. H. Clench, RS), and considered fairly common in spring and fall and less numerous in winter in the Lee Stocking Island–Great Exuma region (JBD et al.). One I saw on Shroud Cay on 4 June 1991 is an unusual summer record.

Prothonotary Warbler (*Protonotaria citrea*).—Nonbreeding visitor. One seen on Great Exuma, 10 August 1968 (R. W. Northridge in Bond 1970).

Worm-eating Warbler (*Helmitheros vermivorus*).—Nonbreeding visitor. One seen on Highborne Cay on 17 December 1990 (DWB), and recorded on Great and Little Exuma (PR-L in Bond 1968).

Ovenbird (*Seiurus aurocapillus*).*—Nonbreeding visitor. Singles seen at Allen's, Highborne, Waderick Wells, and Halls Pond cays during 15–19 December 1990 (DWB), another on Wax Cay on 22 April 1991 (RS), and others in the Lee Stocking Island–northern Great Exuma region occasionally in spring and fall, less often in winter (JBD et al.).

Northern Waterthrush (*S. noveboracensis*).*—Nonbreeding visitor. One seen on Wax Cay on 22 April 1991 (RS), and others in the Lee Stocking Island–northern Great Exuma region occasionally in spring and fall, less often in winter (JBD et al.).

Louisiana Waterthrush (*S. motacilla*).—Nonbreeding visitor. Singles seen on Great Exuma on 16, 18, and 25 July, and one on Little Exuma, 30 July 1991 (DWB), and recorded on "Great and Little Exuma" by PR-L (in Bond 1968).

Common Yellowthroat (*Geothlypis trichas*).*—Nonbreeding visitor. A male and female seen on Allen's Cay on 19 December 1990 (DWB), singles on Wax Cay on 22 April and Hawksbill Cay on 23 April 1991 (RS), and

others in the Lee Stocking Island–northern Great Exuma region occasionally in spring and fall, less often in winter (JBD et al.).

Bananaquit (*Coereba flaveola*).—Very common resident throughout. Breeding.—A nest with one egg, Bells Cay, 25 May, another with three eggs, Stocking Island, 5 July, and many recently fledged young throughout the chain during late May–early August 1991 (DWB); a nest with two ca one-week-old nestlings and one abortive egg, U Key (=Southwest Allen's Cay), 10 April 1893 (Maynard 1895:564); young seen in the Lee Stocking Island–northern Great Exuma region in July (JBD et al.); and "nesting" on Norman's Cay on 31 March 1907 (Chapman 1908:202) and on Hawksbill Cay and Waderick Wells Cay during April–May 1991 (RS).

Stripe-headed Tanager (*Spindalis zena*).—Scarce to uncommon resident on Great Exuma—up to five in one day during July 1991 (DWB), most of the sightings being toward the end of the month when singing males were more evident. The only records for the cays are two seen on Waderick Wells Cay on 15 December 1990 (none during 20 May–27 June 1991) and several in a heavily wooded col on Highborne Cay, 17 December 1990 (DWB). To the best of my knowledge, all previous reports of *S. zena* from the Exumas are based upon a male *S. z. zena* collected at Roseville (=Rolleville), Great Exuma by C. J. Maynard on 21 March 1915 (MCZ 68544).

Indigo Bunting (*Passerina cyanea*).—Nonbreeding visitor. One seen on Wax Cay on 22 April 1991 (RS), others on Lee Stocking Island occasionally in spring (JBD et al.), and recorded on "Great and Little Exuma" (PR-L in Bond 1968).

Painted Bunting (*P. ciris*).*—Nonbreeding visitor. One seen on Highborne Cay, 17 December 1990 (DWB), and others in the Lee Stocking Island-Great Exuma region occasionally in spring and winter (JBD et al.).

Black-faced Grassquit (*Tiaris bicolor*).—Common resident on Great and Little Exuma, but generally uncommon (but widespread) in the cays, being scarce or absent on some; unrecorded on Waderick Wells Cay and Halls Pond Cay among the more thoroughly surveyed islands. Usually seen in casuarinas (*Casuarina equisetifolia*) and in weedy or grassy areas. Breeding.—A nest (one egg) on Shroud Cay on 4 June, another under construction on Lee Stocking Island on 1 July, and a male and female at a nest on Great Exuma, 7 July 1991 (DWB), and an "incubating" female (MCZ 68586) collected on Harvey's Cay by C. J. Maynard, 16 March 1915.

Greater Antillean Bullfinch (*Loxigilla violacea*).—Common to very common resident on Highborne Cay and from Rudder Cut Cay southward to Little Exuma, but unrecorded elsewhere. The distributional hiatus in the cays is unexpected as seemingly suitable habitat is available and ob-

vious competitors are lacking. Possibly limited space and resources in the cays provide only marginal habitat, the southern cays sustaining populations perhaps because of their proximity to potential recruits from Great Exuma, whereas proximity to populations on Eleuthera and a lush (albeit limited) area of woodland may contribute to the success of *L. violacea* on Highborne Cay. Breeding.—A nest with five eggs, Great Exuma, 8 July 1991 (DWB).

Northern Oriole (*Icterus galbula*).*—Nonbreeding visitor. One seen at Barateerre in December 1988 (JBD et al.) and another at Staniel Cay in 1990 (J. Mann).

DISCUSSION

Excluding fossils, at least 125 species of birds are known from the Exumas (126 if two species of cormorants occur). Of the 50 probable breeders, 25 are land birds, two of them (Rock Dove and Common Peafowl) being introductions. Fourteen are shorebirds (including gulls and terns), three are herons and egrets, two are ducks, two others are rallids, and the remaining four are a grebe, shearwater, tropicbird, and Osprey. At least nine others (all waterbirds) that breed elsewhere in the Bahamas and possibly in the Exumas are the Pied-billed Grebe, Double-crested Cormorant (or Neotropic Cormorant or both), Great Egret, Snowy Egret, Little Blue Heron, Reddish Egret, Cattle Egret, Ruddy Duck, and Snowy Plover.

Breeding is documented by observations of nests, eggs, and young for 32 of the 48 indigenous residents or summer visitors, 21 for the first time in the Exumas; all the land birds are listed in Table 1. Summer appears to be the peak breeding season for most species. During 20 May–2 August 1991, I found breeding in progress in 16 (64%) of the 25 species of waterbirds and 11 (49%) of 23 land birds. The only fall and winter breeding records are for the West Indian Whistling-Duck and Osprey.

Thirteen species of fossils (all from Little Exuma) have been discussed by Olson and Hilgartner (1982). The Key West Quail-Dove and Burrowing Owl are the only ones still resident in the Exumas and the Red-legged Thrush may be vagrant there. The giant hawk, *Titanohierax gloveralleni* and the giant barn owl, *Tyto pollens* are extinct. Four species are extant elsewhere in the Bahamas, the Antilles, or in continental North America (Sharp-shinned Hawk [*Accipiter striatus*], Scaled Pigeon [*Columba squamosa*], Cuban Crow [*Corvus nasicus*], and West Indian Woodpecker [*Melanerpes superciliaris*]), and a hawk (*Buteo*), snipe (*Capella*), flicker (*Colaptes*), and meadowlark (*Sturnella*), all unassigned as to species, have congeners in these regions.

I regard records of 14 additional species mentioned in Bond's check-

TABLE 1

INDIGENOUS, BREEDING LAND BIRDS OF THE EXUMAS LISTED IN DECREASING ORDER OF THEIR ABUNDANCE ON GREAT EXUMA

Species	Birds/km[a]	Abundance[b]	
	Great Exuma	Great Exuma	Exuma Cays
Bananaquit (*Coereba flaveola*)	4.4	VC	VC
Bahama Mockingbird (*Mimus gundlachii*)	4.3	VC	VC[c]
Thick-billed Vireo (*Vireo crassirostris*)	3.7	VC	VC
Greater Antillean Bullfinch (*Loxigilla violacea*)	3.7	VC	C[d]
Common Ground-Dove (*Columbina passerina*)	2.7	C-VC	C
White-crowned Pigeon (*Columba leucocephala*)	2.4	C-VC	C
Black-faced Grassquit (*Tiaris bicolor*)	1.5	C	UC
Antillean Nighthawk (*Chordeiles gundlachii*)	0.2	C	C
Gray Kingbird (*Tyrannus dominicensis*)	1.3	FC-C	FC
Black-whiskered Vireo (*Vireo altiloquus*)	0.9	FC	UC
Mangrove Cuckoo (*Coccyzus minor*)	0.6	FC	S
Smoooth-billed Ani (*Crotophaga ani*)	0.5	FC	S
Bahama Woodstar (*Calliphlox evelynae*)	0.4	FC	UC-FC
Northern Mockingbird (*Mimus polyglottos*)	0.4	UC-C	C[e]
Mourning Dove (*Zenaida macroura*)	0.3	UC	nr
Zenaida Dove (*Zenaida aurita*)	0.2	UC	FC
American Kestrel (*Falco sparverius*)	0.0	UC	S[f]
Yellow Warbler (*Dendroica petechia*)	0.0	UC	UC
Stripe-headed Tanager (*Spindalis zena*)	0.1	S-UC	S[g]
White-winged Dove (*Zenaida asiatica*)	0.0	S	nr
Key West Quail-Dove (*Geotrygon chrysia*)	0.0	R	R
Burrowing Owl (*Speotyto cunicularia*)	0.0	R	R
Barn Owl (*Tyto alba*)	0.0	R	R

[a] The number of birds seen and heard/km during surveys covering 112 km.
[b] VC = very common, C = common, FC = fairly common, UC = uncommon, S = scarce, R = rare, nr = no record. Abundance in the Exuma Cays (islands north of Baraterre) is based on general observations only.
[c] One of the most common species in the Exumas overall, but unexpectedly absent or scarce on many islands.
[d] Common on Highborne Cay and from Rudder Cut Cay southward through the chain, but unrecorded elsewhere.
[e] Locally common especially in some of the settlements, but absent or scarce on many islands.
[f] Recorded only on Lee Stocking Island.
[g] Recorded only on Highborne Cay and Waderick Wells Cay.

list supplements as questionable. Eleven were submitted by P. Rodgers-Lee (Bond 1968), then a recent arrival to the Exumas and unfamiliar with Bahaman and North American birds—Lesser Golden-Plover (*Pluvialis dominica*), Wilson's Phalarope (*Phalaropus tricolor*), Forster's Tern (*Sterna forsteri*), Acadian Flycatcher (*Empidonax virescens*), Tree Swallow (*Tachycineta bicolor*), Bahama Swallow (*T. cyaneoviridis*), Bank Swallow (*Riparia riparia*), Loggerhead Shrike (*Lanius ludovicianus*), Nashville Warbler (*Vermivora ruficapilla*), Canada Warbler (*Wilsonia canadensis*),

and Grasshopper Sparrow (*Ammodramus savannarum*). The other sight records relegated to hypothetical status are American Bittern (*Botaurus lentiginosus*) and Forster's Tern on Great Exuma (Bond 1964), and Common Tern (*Sterna hirundo*) on Stocking Cay (=Stocking Island) (Bond 1978).

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AVIAN DISTRIBUTION AND ABUNDANCE RECORDS FOR THE SIERRA DE LOS TUXTLAS, VERACRUZ, MEXICO

KEVIN WINKER,[1,2] RICHARD J. OEHLENSCHLAGER,[3] MARIO A. RAMOS,[4] ROBERT M. ZINK,[5] JOHN H. RAPPOLE,[2] AND DWAIN W. WARNER[1]

ABSTRACT.—Between 1973 and 1987 we spent more than 36 months studying birds in the Sierra de Los Tuxtlas, on the Gulf coast of southern Veracruz, Mexico. This area contains the northernmost tropical rainforest in the western hemisphere, and has undergone relatively rapid deforestation in the past three decades. Its avifauna is diverse, consisting of both resident and migratory birds. We recorded 405 species, including 58 that have not been reported from the region before, as well as several that apparently have not been reported for Veracruz. Fully 350 species are documented by specimens; the remaining 55 consist of sight records only. We compare our results with past surveys of Los Tuxtlas and discuss 124 species whose status in the region is affected by our data. Of the 405 species we recorded in Los Tuxtlas, 96 (23.7%) appear on a list of bird species from the northern neotropics thought to be in danger due to tropical deforestation. *Received 9 Jan. 1992, accepted 29 April 1992.*

The Sierra de Los Tuxtlas (hence Los Tuxtlas) is a rugged, mountainous region of volcanic origin, isolated from the Sierra Madre Oriental range by extensive lowlands. It is near the Gulf of Mexico on the western side of the Isthmus of Tehuantepec in southern Veracruz, Mexico. Los Tuxtlas, approximately 4200 km^2 in areal extent, contains the northernmost tropical rainforest in the western hemisphere (Andrle 1964, Pennington and Sarukhan 1968, Dirzo and Garcia 1992). The recorded avifauna includes more than 400 species. Although only one of these 400+ species (Long-tailed Sabrewing [*Campylopterus excellens*]) is endemic to the region, Los Tuxtlas is known for its endemic subspecies (Binford 1989). These endemic subspecies are *Geotrygon lawrencii carrikeri, Empidonax flavescens imperturbatus, Myioborus miniatus molochinus, Atlapetes brunneinucha apertus,* and *Chlorospingus ophthalmicus wetmorei* (see Wetmore 1943: 225, Lowery et al. 1949:8, and Andrle 1967). In addition, a specimen from Los Tuxtlas has recently been designated the type of *Vireolanius pulchellus ramosi,* a subspecies endemic to the Isthmus of Tehuantepec region (Phillips 1991).

Previous ornithological surveys of Los Tuxtlas are encompassed or

[1] Bell Museum of Natural History, 10 Church St. SE, Univ. Minnesota, Minneapolis, Minnesota 55455.
[2] National Zoological Park, Conservation & Research Center, Front Royal, Virginia 22630.
[3] The Science Museum of Minnesota, 30 East 10th Street, Saint Paul, Minnesota 55101.
[4] Environmental Assessment & Programs Division, The World Bank, 1818 H Street NW, Washington, D.C. 20433.
[5] Museum of Natural Science, Louisiana State Univ., Baton Rouge, Louisiana 70803.

summarized by Loetscher (1941, 1955), Wetmore (1943), Lowery et al. (1949), Lowery and Dalquest (1951), Edwards and Tashian (1959), and Andrle (1964, 1966, 1967). This report summarizes the results of over 36 months of field effort in Los Tuxtlas between 1973 and 1987 and provides information on the occurrence and abundance of selected bird species. An 18-month, locally intensive ornithological survey (1973–1975) of the Gulf of Mexico lowlands and lower elevations of the area E and NE of Volcán San Martín (ca 28 km N of Catemaco, Veracruz) forms the basis of this paper. Later work, including areas on and near Volcán Santa Martha (see Winker et al. 1990a, b; Rappole et al. 1992) augments the original survey.

STUDY AREA AND METHODS

The primary study area E and NE of Volcán San Martín is bounded by a line from the Gulf coast directly west to the town of Balzapote, southwest to Laguna Escondida, southeast to the village of Sontecomapan, and eastward to the Gulf coast. This is a region of diverse physiographic features. Coastal beaches of volcanic sand are interrupted by weathered lava cliffs partially covered with dense vegetation. Brackish and freshwater marshes and swamps grade into lowland wet pastures, especially between the coast, the shores of the Laguna de Sontecomapan, and the flanks of the Volcán San Martín. Surveys of the avifauna on higher-elevation slopes were restricted to relatively short visits to Volcán Santa Martha in 1985 and 1986. As in many tropical lowland areas today, the region consists of a mosaic of habitats ranging from mature rainforest (diminishing rapidly) to pastures, with much agricultural and second-growth habitat, the latter ranging from sparse, low shrubs, to dense, tall *Cecropia-Ochroma* woodlands. Andrle (1966) estimated that half of Los Tuxtlas was still forested in 1962; using Landsat images and air photos, we estimated that only 15% was still forested in 1986 (Winker et al. 1990a; cf Dirzo and Garcia 1992).

During the basic survey spanning Aug. through May, major effort (netting and observation) was concentrated at and adjacent to the Estación de Biología Los Tuxtlas of the Instituto de Biología, Univ. Nacional Autonoma de México (hereafter referred to as "the Station"), which is 0.5 km W of Cerro Balzapote and at another site 1.5 km E of Cerro Balzapote (Playa Escondida). At the Station, three sites within 1.5 km of one another were studied intensively: primary rainforest, 15-yr-old *Cecropia-Ochroma* forest, and a recently cleared field-rainforest edge.

A total of 62,742 mist net-h was obtained at the Station, 34,074 net-h at the primary rainforest site, 8946 net-h at the secondary forest site, and 19,722 net-h at the rainforest-field site. Also, nets were operated for 14,663 net-h in areas of dry second-growth, lowland swamp, and various forest habitats in and around the Station and at Agua Dulce behind the village of Jicacal (next beach SE of Playa Escondida); 6369 net-h were obtained in forest at the Station at night. Many hours were spent observing and collecting specimens near the Playa Escondida motel in areas of bamboo, riparian thickets, lowland pastures, ponds, and coastal beach (at and near Jicacal). The vegetation of the Station and surrounding area is described by Andrle (1966, 1967), Ramos and Warner (1980) and Ramos (1983, and references therein).

Other study sites where intensive mist netting was conducted in the 1980s were in the Sierra de Santa Martha, low mountains around and near the Volcán Santa Martha. The La Peninsula site, approximately 5.5 km ENE of Coyame, was located in the Coxcoapan River

Valley (elev. ca 150 m), where over 38,600 net-h were obtained (1982–1986, primarily Oct. through Apr.). Work near the crater of Volcán Santa Martha, approx. 15 km ESE of the La Peninsula site, was conducted 4–21 Mar. 1985 (elev. 470–950 m; ca 830 net-h). Descriptions of the La Peninsula and the lower elevation Santa Martha sites can be found in Winker et al. (1990a). At El Bastonal we used another site in the Coxcoapan River Valley, about 5.5 km SSE of the La Peninsula site (elev. ca 400 m). This site was netted intensively Jan.–Mar. 1986 for a total of 10,067 net-h. The vegetation at this site did not differ greatly from that of the La Peninsula site. For maps of the areas studied, see Andrle (1967), Rappole and Warner (1980), and Winker et al. (1990a).

Andrle (1967) discussed 250 species of resident (or indigenous) birds known to have occurred in Los Tuxtlas. Because we compare our observations to his findings, we use his abundance categories: *abundant* (A)—over 150 recorded every day; *very common* (VC)—75 to 150 recorded every day; *common* (C)—15 to 75 recorded every day; *fairly common* (FC)—five to 15 recorded every day; *rather uncommon* (RU)—three to eight recorded but not every day; *uncommon* (U)—one to five recorded, but frequently not observed for one or a few days at a time; *very uncommon* (VU)—one to five recorded in one to three months and usually not observed for one to three weeks at a time; *rare* (R)—less than ten recorded per year and not recorded at all for varying, sometimes prolonged periods; *very rare* (VR)—recorded from one to three or four times in the region and likely to occur again. For brevity, where possible we give Andrle's abundance designation after a resident species name. If a species was not recorded by Andrle (1966, 1967), we denote it as NR, and thus report the first record for Los Tuxtlas (new records not supported by specimens are referred to as NR*). Andrle (1966) discussed 67 of the 131 migrant bird species previously recorded from Los Tuxtlas. He (1966) did not use the abundance categories of his 1967 paper, but provided more general descriptions, which we use. Migrants observed by us but not recorded by Andrle (1966) or other workers for Los Tuxtlas are also denoted as NR. Our records corroborate Andrle (1966, 1967) for the occurrence and abundance of the species that he discussed but which we do not.

Our work was documented by observation, capture, and/or collection. Most voucher specimens are housed in the Bell Museum of Natural History (Univ. of Minnesota, Minneapolis, Minnesota), but some were left in Mexico. We include specimen data where we think it is useful, but do not give exhaustive treatments. If desired, more data can be had by examining the specimens themselves or by requesting information from the authors or the Curator of Birds at the Bell Museum of Natural History.

SPECIES ACCOUNTS

We recorded 405 species of birds. At least one specimen was obtained of each of 350 species; the remaining species were documented by sight records only. The species and data discussed below were chosen because they represent new and significant information on the avifauna of the region. Unless noted (e.g., NR*, sightings), all species discussed here are documented by specimens.

Brown Booby (*Sula leucogaster*). NR*. One individual was seen offshore at Jicacal during a storm on 4 Sept. 1974.

Bare-throated Tiger-Heron (*Tigrisoma mexicanum*). NR. Occasionally seen perched in low trees in open, wet pasture near swamps in the lowlands surrounding the Laguna de Sontecomapan. An adult female in breeding

condition perched with another bird was collected on 7 May 1975. Stomach contents included common eel (*Anguilla anguilla*).

Cattle Egret (*Bubulcus ibis*). U. Since Andrle's study, Cattle Egrets have increased in abundance in Los Tuxtlas; our estimate of their abundance is VC. We have seven specimens and thousands of sightings (17 Sept.–2 June); they seem to breed regularly near the edge of Lake Catemaco.

Fulvous Whistling-duck (*Dendrocygna bicolor*). NR*. A flock of 10–15 was observed 3 Oct. 1974 at Jicacal.

Greater White-fronted Goose (*Anser albifrons*). NR*. A flock of 35 was seen on 10 Dec. 1974.

American Wigeon (*Anas americana*). NR. A female in heavy body molt was taken on 11 Dec. 1974.

Lesser Yellow-headed Vulture (*Cathartes burrovianus*). NR. A female collected on 2 May 1975 (not in breeding condition) had recently eaten immature common eels. One was observed on 27 Apr. 1975. No evidence of wintering was detected; there may be migratory movement of this species through Los Tuxtlas (Apr.–May).

Hook-billed Kite (*Chondrohierax uncinatus*). VR. RJO observed an adult female in shrubby, wet lowlands near La Palma on 3 May 1974.

Snail Kite (*Rostrhamus sociabilis*). RU. Although individuals could be seen regularly in trees in and near low, wet pasture in the early 1980s (Dec.–Mar.), we had only one sighting in the same areas in the late 1980s, suggesting a decline in abundance (R).

Double-toothed Kite (*Harpagus bidentatus*). VR. We collected a male on 5 Jan. 1974 and an immature female 24 Oct. 1974 in primary rainforest near Playa Escondida; both stomachs contained orthopteran remains. Two individuals were perched in a tree on 6 Mar. 1974 at the Station, and other sightings occurred on 4 Jan. 1983 (rainforest edge) and 16 Mar. 1985 (deep within primary rainforest at 800 m). The only previous record is a bird seen at Dos Amates on 17 Mar. 1960 (Andrle 1967).

Black-collared Hawk (*Busarellus nigricollis*). NR*. An individual was seen leaving a low perch near a pool on the Coxcoapan River (near La Peninsula) on 19 Jan. 1985.

Solitary Eagle (*Harpyhaliaetus solitarius*). NR*. A flying, calling immature was seen from above on a high ridge near Volcán Santa Martha on 4 Mar. 1985. There are other recent sight records for Los Tuxtlas (W. J. Schaldach, Jr., pers. comm.).

Broad-winged Hawk (*Buteo platypterus*). Andrle (1966) considered this species a common migrant in Mar. and Apr. but his only autumn dates were from Oct. Our sightings were from 22 Sept., 15 Nov. (adult), 19 Dec., Jan. (6, 17, 27), and Feb. (10–11, 14, 21, 26–28), and indicate wintering in low numbers.

Short-tailed Hawk (*B. brachyurus*). Andrle (1967) cited three records, and noted two more (1968) on 8 Oct. 1960 near Corral Nuevo on Hwy 180. We add observations of single birds at the edge of primary rainforest on 31 Dec. 1973, and 13 and 23 Feb., 23 Sept., 21 Oct., and 17 Dec. 1974, 4 Jan. 1983, and soaring over rainforest in Nov. and Dec. 1984.

White-tailed Hawk (*B. albicaudatus*). NR*. A species likely to have both resident and migrant individuals occurring in the state of Veracruz (Loetscher 1941), it nevertheless does not seem to have been previously recorded from Los Tuxtlas. A single bird in full adult plumage was seen by KSW soaring at low elevation near El Bastonal in the last week of Feb. 1986.

Zone-tailed Hawk (*B. albonotatus*). VR. We have more than 37 sightings from 21 Nov.–26 Apr. The bird observed on 26 Apr. was calling. These data suggest overwintering and a U status.

Black Hawk-Eagle (*Spizaetus tyrannus*). VR. Andrle (1967) noted three records for Los Tuxtlas. We found the species to occur regularly in the rainforest of the Coxcoapan River Valley (La Peninsula and El Bastonal sites), where individuals could be seen several times per week flying, soaring, and calling loudly overhead (Dec.–Mar.). Confined to rainforest, its status in this habitat could be considered RU.

Orange-breasted Falcon (*Falco deiroleucus*). NR*. Exceedingly rare; we have one sight record (4 Mar. 1985). W. J. Schaldach, Jr. (pers. comm.), has recorded breeding at El Faro (near La Perla del Golfo), 30 km east of La Barra, in July.

Peregrine Falcon (*Falco peregrinus*). Andrle (1966) mentioned only four records of this species for Los Tuxtlas. We have over 50 records (21 Sept.–3 May), with at least one sighting for each month between these dates. RJO observed 13 birds on 25 Sept. 1974. Most individuals were seen along the coast near Playa Escondida, and all birds observed closely were adults.

Plain Chachalaca (*Ortalis vetula*). This species was considered VU in Andrle (1966) but as C in Andrle (1964); we agree with the latter designation. A female incubating four eggs was found on 5 May 1975; the nest was located 2 m above the ground in a bush located on a hillside covered by brush of variable density. Other breeding females were taken on 15 and 28 Apr.

Ruddy Crake (*Laterallus ruber*). VU. R. W. Dickerman (in Andrle 1967) heard this species at Arroyo Agrio marsh from 22 July to 9 Aug., and on 3 Sept. 1963. RJO noted it regularly in substantial numbers in lowland marshes 5 km south of Cerro Balzapote and five specimens were collected (26–28 Apr., 2 May). Observations included an individual climbing about in brushy vegetation at 2.5–3 m. In addition, a juvenile (nearly adult-

sized) was collected at Dos Amates on 20 July 1964 by R. W. Dickerman (specimen in Bell Museum).

Yellow-breasted Crake (*Porzana flaviventer*). NR. A male with enlarged testes (1 = 9 × 3.5 mm) was collected on 3 Feb. 1974 in a marshy pasture near La Palma. It had eaten small crabs. Also, R. W. Dickerman collected a male at Dos Amates on 2 May 1964 (specimen in Bell Museum).

Common Moorhen (*Gallinula chloropus*). Andrle (1966) cited only spring records for Los Tuxtlas. Our specimen taken 20 Dec. 1974 is apparently the only winter record.

Limpkin (*Aramus guarauna*). U. Locally common in wet pastures and dense, shrubby swamps (one specimen and many sight records).

Semipalmated Plover (*Charadrius semipalmatus*). NR. Our five specimens, taken 21 Sept.–25 Feb. (four female, one "female?"), are the first records for Los Tuxtlas. The only other apparent record for Veracruz is a male taken by R. W. Dickerman near Tlacotalpan on 27 Apr. 1963 (specimen in Bell Museum).

Piping Plover (*C. melodus*). NR. Two females collected 10 Feb. and 4 Aug. 1974 were with small flocks of Wilson's (*C. wilsonia*) and Snowy (*C. alexandrinus*) plovers. These records of *C. melodus* are the first for Veracruz. We had one sighting on 24 Jan. 1983 (for more recent sightings in Veracruz, see Haig 1987).

American Avocet (*Recurvirostra americana*). NR. Two specimens were taken, one on 28 Sept. (female) and another 17 Oct. 1974 (male).

Greater Yellowlegs (*Tringa melanoleuca*). NR*. Present locally in small numbers, probably throughout the winter. Our sightings are 2–3 Oct., 12 Jan. (flock of five), and 30 Mar.

Solitary Sandpiper (*T. solitaria*). RU. Loetscher (1955) noted few Veracruz specimens, and Andrle (1966) did not comment on the species. We encountered it regularly at Playa Escondida in low, wet pastures (many sightings Dec.–Feb.). Two specimens were taken on 30 Mar. and 23 Apr. 1975.

Upland Sandpiper (*Bartramia longicauda*). NR. An extremely fat female was collected on 16 Oct. 1973 near coastal beach. We had additional sightings on 5, 15 (two), and 20 Apr. 1974.

Long-billed Curlew (*Numenius americanus*). NR*. Sightings occurred on 5 (two) and 20 Sept., and on 7 Dec. 1974 (two).

Baird's Sandpiper (*Calidris bairdii*). NR. Three specimens were taken 3 Oct. (im. male), 5 and 6 Apr. 1974 (females), and one was seen on 7 May 1974.

Pectoral Sandpiper (*C. melanotos*). NR. Specimens were taken on 23 Oct. 1974 (male), and 18 May 1975 (one male, one female).

Semipalmated Sandpiper (*C. pusilla*). NR. Our 13 specimens, taken on

22 Aug., 21 Sept. (two), 14 Oct., 5 Apr. (seven), and 6 Apr. (two) suggest that this species is regular along the coast in migration (see Thompson 1958). Individuals were collected along the beach near Jicacal. Specimen records for this species do not seem to have been previously reported from Veracruz. From specimens in the Bell Museum we note one other for Los Tuxtlas (Laguna de Sontecomapan, 13 May 1962, Abraham Ramírez V.), one from near Lerdo de Tejada (16 Sept. 1963, R. W. Dickerman), and four from near Tlacotalpan (9 Aug. 1961 [three], and 7 Apr. 1962, R. W. Dickerman).

Western Sandpiper (*C. mauri*). NR. We have many sightings and 11 specimens, taken 22 Aug.–15 Apr., showing that this species is a regular migrant along the Gulf coast of Mexico and probably winters in low numbers in the Los Tuxtlas area.

Dowitcher species (*Limnodromus* sp.). NR*. Two dowitchers seen at a pond edge in low, wet pasture on 27 Dec. 1986 were identified as probably *griseus* by vocalizations given upon flushing. Another sighting of an unidentified dowitcher occurred on 13 Feb. 1983.

Common Snipe (*Gallinago gallinago*). NR. A female was taken on 3 Feb. 1974 in a wet, swampy pasture.

Wilson's Phalarope (*Phalaropus tricolor*). NR. A lone female was taken on the beach near Jicacal on 22 Aug. 1974. Andrle (1968) noted two near Alvarado on 3 May 1952.

Franklin's Gull (*Larus pipixcan*). Andrle (1966) noted that this species is a fairly common spring migrant in Los Tuxtlas, but his only autumn date was 17 Sept. 1962. On 9 Dec. 1974, RJO saw two flocks totalling 15–20 birds. Our other observations corroborate Andrle's spring dates.

Sooty Tern (*Sterna fuscata*). NR. The first records for Veracruz are an immature observed offshore from Jicacal on 8 Dec. 1973 and the remains of two adults (27 Feb. and 1 Mar. 1974) found on the beach at Jicacal.

White-winged Dove (*Zenaida asiatica*). Loetscher (1955) found this species only in the most arid parts of Veracruz, and Andrle (1967) considered it rare in Los Tuxtlas. Our observations suggest a strong migratory presence in spring and autumn near the coast. In autumn we have sighting and specimen records from 21 Oct. to 6 Nov. (600–700 seen in flocks of 5–100 on 6 Nov.), and in spring from 6 to 28 Apr.

Common Ground-Dove (*Columbina passerina*). VR. Previously reported only by Sclater in 1857 (in Andrle 1967). Our seven specimens (from Nov., Apr., and May) and several sightings indicate that this species is now more common, probably as a result of deforestation and the subsequent availability of more open habitats. A gap in our observations between Nov. and Apr. suggests a winter movement out of Los Tuxtlas.

Plain-breasted Ground-Dove (*C. minuta*). VR. Nine were collected (20

Dec.; 25 Jan.; 12 [two], 25 [two], 30 [two] Apr.; 23 May) and others were seen in wet, shrubby lowland pastures, often bordering swampy areas. Females taken in Apr. were in breeding condition.

Brown-hooded Parrot (*Pionopsitta haematotis*). VR. Reported only from Lake Catemaco (Davis 1972, Edwards and Tashian 1959). Our four male specimens, some from small flocks, were taken 11 Dec. and 17 and 22 Jan. Sightings include (date and number of individuals): 7 (one), 17 (eight–ten), 22 (four), and 24 (four) Aug.; 22 (three) and 23 (three) Nov.; 12 (13) Jan.; 4 (16), 5 (four), 16 (two) Feb.; 12 (six), 25 (two) Mar.; 13 (three), 15 (one), 25 (two), 26 (two–three) Apr.; 5 (two), 6 (two), 23 (seven), and 27 (two) May. These sightings may represent a small (ca 15) resident population. This species was most frequently encountered in tall, dense, mature secondary forest, and at the edge of primary rainforest.

Mangrove Cuckoo (*Coccyzus minor*). Andrle (1967) cited one record. Four specimens (10, 14, 27 Jan. and 13 Apr.) were collected along the edge of disturbed primary rainforest remnants, in 6 m tall *Solanum* sp. with sparse trees, and in or near coastal dune vegetation. Additional sightings occurred 27 Nov. and 25 Dec.

Pheasant Cuckoo (*Dromococcyx phasianellus*). NR. Two males were collected near Cerro Balzapote in dense, wet, brushy areas: one (skull unossified, heavy molt) on 29 Oct. 1973, and another (skull 50% oss., wing molt) on 11 Oct. 1974. Bruce A. Fall and MAR observed a displaying male near Playa Escondida in Mar. Several males were heard and seen displaying at 500–800 m on Volcán Santa Martha in Mar. 1985, and one was heard singing on 13 Mar. 1986 near El Bastonal in oak-sweet gum forest.

Crested Owl (*Lophostrix cristata*). NR*. One individual was heard and seen on 14 Mar. 1985 at 800 m on Santa Martha; another was heard on 9 Mar. 1986 at La Peninsula (ca 150 m).

Spectacled Owl (*Pulsatrix perspicillata*). VR. Previously reported only by Sclater (1857 in Andrle 1967) at Sontecomapan. A male (610 g, with body and secondary molt) was found dead on the road at the Station on 25 Aug. 1974; the stomach contained a small crab. Individuals were seen repeatedly (once two simultaneously) in Jan. and Feb. 1985 at La Peninsula.

Least Pygmy-Owl (*Glaucidium minutissimum*). NR*. Very rare. Probably the same individual was seen repeatedly in early Jan. 1984 in rainforest at La Peninsula.

Black-and-white Owl (*Ciccaba nigrolineata*). NR*. Calls attributed to this species were heard in Mar. 1985 on Volcán Santa Martha and repeatedly in Feb. and Mar. 1986 near El Bastonal.

Common Nighthawk (*Chordeiles minor*). The status of this species is

poorly documented for Los Tuxtlas and Veracruz in general. Our experiences were limited to seeing birds and hearing calls given in flight. The following records (date, number of individuals) are based on calling individuals: 26 (one), 27 (one) Mar.; 15 (11), 17 (11), 24 (ten), and 25 (10+) Apr. 1974; 15 (one), 16 (five), 20 (two), 21 (one), 22 (two), 25 (one), 26 (two), and 29 (one) Apr. 1975; 7 (one) May. Autumn dates were 29 (one) Sept. 1974; 20 (nine) and 29 (nine) Oct. 1974; 24 (one) Nov. 1973. Silent individuals seen at considerable heights on 22 Aug. 1973, 1 Apr. 1975, and 1 May 1975 were probably this species.

Tawny-collared Nightjar (*Caprimulgus salvini*). NR. Frequently heard singing on pasture-rainforest edge at El Bastonal (late Jan.–mid-Mar. 1986), and at La Peninsula (6, 20, and 26 Feb., and 5 Mar.). A road kill was found near El Bastonal on 22 Feb. 1986.

White-necked Jacobin (*Florisuga mellivora*). NR. Four females were taken on 6 Jan. (wing molt), 25 Feb., 14 Mar., and 16 Apr. (immature plumage) at the clearing edge near the Station.

Blue-throated Goldentail (*Hylocharis eliciae*). NR. We collected a female on 16 Apr. in one-year-old second-growth and a male (?) on 13 Apr. in primary forest adjacent to the Station.

Tawny-winged Woodcreeper (*Dendrocincla anabatina*). We handled 69 individuals at the Station and 42 at La Peninsula. Andrle (1967) listed this species as VU; we consider it RU.

Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*). NR. This species was not mentioned by Andrle (1967). We examined 63 individuals at the Station and 14 were banded at La Peninsula, most from primary rainforest (Aug.–May). Females in mid-Aug. had old brood patches. They are permanent residents, and should be considered U to RU.

Great Antshrike (*Taraba major*). VR. Andrle (1967) knew of two records from near Sontecomapan. Two specimens were obtained in wet, dense second-growth, 4.5 km ESE of Cerro Balzapote on 2 and 24 Apr. 1975.

Dusky Antbird (*Cercomacra tyrannina*). NR*. A female was captured and banded at La Peninsula on 6 May 1985. Another female, probably of this species, was captured on 26 Oct. 1983 and briefly handled, but escaped.

Eastern Phoebe (*Sayornis phoebe*). Andrle (1966) reported one record for Los Tuxtlas. We collected five birds (13 and 27 Nov., 10 Dec. and 9 Feb.) and saw several in pastures with open shrub growth, often near ponds. Our specimens plus sightings in Dec. and Jan. suggest that the species is an uncommon winter resident.

Say's Phoebe (*S. saya*). NR. A male was collected on 21 Dec. 1974 in an open pasture (closely grazed) with exposed rocks.

Western Kingbird (*Tyrannus verticalis*). The first reported records for Veracruz noted by Andrle (1966) and Amadon and Eckleberry (1953) were misidentified and were actually "Tropical" Kingbirds (*T. melancholicus/couchii*) (RJO, *in litt.* from J. Farrand, Jr., and Allan R. Phillips, pers. comm., respectively). A very fat female with insects and fruit pits in its stomach was collected on a shrubby hillside on 8 May 1975, 4.5 km SEE of Cerro Balzapote.

Couch's Kingbird (*T. couchii*) and Tropical Kingbird (*T. melancholicus*). Traylor (1979) concluded that Tropical and Couch's kingbirds are distinct species. Based on vocalizations, both forms occur in the lowland areas we surveyed, and both species are represented in our specimen sample. The local breeding status of *T. couchii* is uncertain; calling birds were heard from 19 Apr. to 2 May. *T. melancholicus* is a local permanent resident and breeder.

Acadian Flycatcher (*Empidonax virescens*). Andrle (1966) noted a single specimen for Los Tuxtlas (Catemaco, 13 Oct. 1950), and Loetscher (1955) reported the only other apparent record for Veracruz (10 May 1901 at Jalapa, by Nelson and Goldman). We captured or collected a total of 59 specimens near the Station and handled an additional 15 at La Peninsula 11 Sept.–1 Nov., and 30 Mar.–28 May. Based on netted and collected specimens, approximate peaks in migration were late Sept.–early Oct., and late Apr.–early May. Habitats ranged from primary rainforest to brushy slopes. These specimens clearly show that the species has been overlooked in past surveys, both as a spring and autumn migrant. There was no evidence of wintering.

Alder Flycatcher (*E. alnorum*) and Willow Flycatcher (*E. trailii*). The migration of these two species through Los Tuxtlas is unclear because Andrle's studies predated their separation (A.O.U. 1973), and field identification is difficult. Andrle (1966) noted that "Traill's" Flycatchers were common autumn migrants, but he had no definite spring records. We handled approximately 350 Willow/Alder Flycatchers (specimens and banding), both in autumn (16 Aug.–8 Nov.) and spring (1–28 May). More than 90 of these birds occurred in spring. Voucher specimens from both seasons include both *trailii* and *alnorum* (*fide* Allan R. Phillips).

White-throated Flycatcher (*E. albigularis*). NR. A male was collected on 10 Apr. and a female on 13 May 1975, in dry, brushy second-growth; neither was in breeding condition.

Yellowish Flycatcher (*E. flavescens imperturbatus*). Both Andrle (1967) and Johnson (1980) cited the elevational range of this species as above 900 m. Our eight specimens (9, 21, 30 Oct., 14 Nov., 9, 23 Dec., and 16 Jan.) were taken near the Station at about 100 m in primary forest. Many of these occurrences coincided with autumn and winter storms, which

drive some species to lower elevations. One bird was seen perched in an *Astrocaryum* palm in disturbed primary rainforest on 22 Nov. 1974, and individuals were observed occasionally in similar habitat at the El Bastonal site in Feb.–Mar. 1986.

Olive-sided Flycatcher (*Contopus borealis*). Andrle (1966) cited it only as a fairly common autumn migrant in Los Tuxtlas. We have numerous sight and specimen records: 17, 24, 25 (two), 26, 27, 28, 29 (three), 30, and 31 Aug., 11, 21, 24, 28, and 30 Sept., 1 (three) 2, 3, 7, 9, 11, 12, 14, 17, 21, 24, 25, 27, 30 and 31 Oct., 2, 20, 22, 23, and 28 Nov., 2 Dec., 20, 27, and 30 Jan., 19 and 23 Feb., 6 Mar., 17 Apr. (in heavy molt), 6 (three), 7, 9, 10, 11, 12, 18, 20, 21, 23 (three), 25 and 31 May. These records suggest wintering in low numbers, but we have only one nominal wintering period specimen (23 Feb.). Most birds were in pastures with isolated remnant forest trees, or in open woodlands and sparse groves. A. R. Phillips (pers. comm.) found the species to be regular in pines above Ocotal Chico in Dec.

Sulphur-rumped Flycatcher (*Myiobius sulphureipygius*). We netted over 180 from Aug. to May, mostly in primary rainforest, where its dense forest haunts make detection difficult. Listed by Andrle (1966) as VU, we suggest FC as its status.

Sepia-capped Flycatcher (*Leptopogon amaurocephalus*). Andrle (1967) noted only one record for Los Tuxtlas and listed its status as VR. Most of the 45 individuals collected or banded were netted from Aug. to May in primary rainforest or adjoining mature secondary forest (RU).

Ochre-bellied Flycatcher (*Mionectes oleagineus*). We handled over 380 individuals from Aug. to May (inclusive), mostly in primary rainforest. We suggest that its status is FC, rather than RU, as considered by Andrle (1967). Females taken 20 Apr. and 28 May were in breeding condition.

Lovely Cotinga (*Cotinga amabilis*). VR. Andrle (1967) reported two birds collected near Dos Amates. We netted a female near the Station in primary rainforest on 5 Feb. 1974. We have other sight records from Dec. through Mar. These records suggest that the species is U rather than VR; it is easily overlooked in the high canopy of dense primary rainforest.

Thrush-like Manakin (*Schiffornis turdinus*). NR. A male was taken on 12 Oct. 1974 at the Station, in primary rainforest.

Violet-green Swallow (*Tachycineta thalassina*). NR*. Loetscher (1941) noted a general absence of authentic Veracruz records, and did not consider the species later (1955). Andrle (1966, 1967) also did not comment on the species. Several flocks were observed at El Bastonal on 15 Mar. 1986.

Bank Swallow (*Riparia riparia*). Andrle (1966) observed this species on only one autumn date (16 Sept.). We have at least 22 records (including

five specimens) between 22 Aug. and 24 Oct., indicating a more common autumn migratory status.

Barn Swallow (*Hirundo rustica*). We found this species to be RU to FC during Jan.–Mar. at El Bastonal; Andrle (1966) noted that there were no winter records.

Cliff Swallow (*H. pyrrhonota*). Although Andrle (1966) reported this species as uncommon, we observed them regularly from 27 Aug. to 7 Oct., including observations of 200+ from 20 Sept. to 4 Oct. 1974. Spring dates were from 2 Apr. to 12 May, and "hundreds" were seen on 10 Apr. 1975.

Marsh Wren (*Cistothorus palustris*). NR. Apparently the first record from Los Tuxtlas, a female in general body molt, was collected on 25 Apr. 1975, 7 km ESE of Cerro Balzapote.

Ruby-crowned Kinglet (*Regulus calendula*). To Andrle's (1966) single record for Los Tuxtlas (30 Oct. 1962 near Ocotal Grande) we add four specimen records (one on 18 Oct. and three on 13 Nov. 1974), and sight records on 28 Dec. 1974 and 3 and 6 Mar. 1986. All were encountered in lowland and highland pastures with shrubby growth.

Tropical Gnatcatcher (*Polioptila plumbea*). NR. Our specimens from 4 Aug., 28 Dec., 20 Mar. (male with enlarged testes), 20 and 21 May are apparently the first for Los Tuxtlas. Additional observations were made on 6, 12 and 30 Oct., 4 Nov., 27 Dec., 25 Mar., and 9 Apr. This species was found in or at the edge of mature rainforest and in tall swamp forest.

Wood Thrush (*Hylocichla mustelina*). Andrle (1966) did not comment on the presence of the Wood Thrush in Los Tuxtlas, and Loetscher (1955) reported the species as uncommon in Veracruz. We found it to be among the most common of forest birds during the winter (see Winker et al. 1990a, b).

Hermit Thrush (*Catharus guttatus*). NR. A first-year male was collected on 11 Jan. 1975 near Playa Escondida; it was identified by A. R. Phillips as *C. g. nanus*. Two others were seen in disturbed primary rainforest on 1 Jan. 1975. Loetscher (1941) mentioned that the only Veracruz specimen from below 1300 m (4000 ft) was a female from Jesús Carranza (24 Jan. 1904); our records corroborate the scarcity of this species in the lowlands.

Veery (*C. fuscescens*). NR. This species seems to have been overlooked by previous investigators. We collected 42 individuals between 22 Sept. and 11 Oct. (all immatures) and 11 between 21 Apr. and 13 May. The spring specimens were mostly not fat. Most birds were netted adjacent to the Station, either in primary rainforest or mature secondary forest.

Northern Mockingbird (*Mimus polyglottos*). To Andrle's (1967) one previous record (2 Apr., Lake Catemaco) we report three birds collected

in lowland thickets and shrubby pastures on 3 Nov. 1973, 27 Jan. and 3 Mar. 1974.

Long-billed Thrasher (*Toxostoma longirostre*). NR*. A calling individual was observed on 11 Dec. 1974 in a pasture with dry clumps of *Solanum* sp.

American Pipit (*Anthus spinoletta*). NR. Three individuals were collected on wet beach sands at Jicacal on 17 Oct. 1974. Phillips (1991) identified two as *A. s. pacificus* and one as *A. s. geophilus.*

Loggerhead Shrike (*Lanius ludovicianus*). NR*. One was seen perched on a roadside utility wire over open agricultural lands near Santiago Tuxtla on 18 Oct. 1973. This is the only report from Los Tuxtlas.

European Starling (*Sturnus vulgaris*). NR. An incubating female was collected on 13 Apr. 1975 at its nest hole in a large, isolated dead tree in a wet lowland pasture 1 km east of La Palma. This occurrence may represent the southernmost nesting of starlings along the eastern coast of Mexico (see Phillips 1991).

White-eyed Vireo (*Vireo griseus*). Andrle (1966) considered this species to be regular but not common as a migrant and winter visitant, most numerous in autumn (first autumn date 4 Oct.). We handled over 215 birds between 22 Sept. and Feb. (inclusive), and observed many others. Our spring records include dates from 2 Mar. to 11 May. This species was frequently encountered in second-growth, and at the edges of pastures and forests.

Bell's Vireo (*V. bellii*). NR. A female taken 16 May 1975 and subsequently identified by A. R. Phillips as *V. b. bellii,* is apparently the first record of this species for Los Tuxtlas. It was found in variably dense, 1–4 m second-growth on a dry south-facing hillside.

Warbling Vireo (*V. gilvus*). Our specimen (12 May 1975) and nine sight records (26 and 28 Nov., 3 Dec., 13, 17, and 18 Feb., 31 Mar., 7 and 30 Apr.) augment the single previous record from Los Tuxtlas cited by Andrle (1966). This species occurred in scattered trees and shrubs in more open habitats, as well as in heavy second-growth.

Philadelphia Vireo (*V. philadelphicus*). Andrle (1966) listed this species as only a rare autumn migrant with three records for Los Tuxtlas. We handled 25 individuals, nine from 3 Oct. to 13 Nov., and 16 from 16 Apr. to 24 May. Nine other sightings were recorded; the latest date was 3 Dec., although a sighting on 16 Feb. might suggest a rare winter presence. Habitats in which this species was encountered resembled those of *V. griseus* and *V. olivaceus.*

Red-eyed Vireo (*V. olivaceus*). Andrle (1966) reported this species as an uncommon autumn migrant (7 Sept. to 24 Oct.) and gave only one

spring date (15 May). We handled over 110 individuals, including 74 from 30 Aug. to 9 Nov. and 36 from 1 Apr. to 28 May. There were numerous additional sightings, including two on 23 Nov., which is the latest autumn date. This species was encountered in second-growth and on the edges of pasture and rainforest.

Yellow-green Vireo (*V. flavoviridis*). C. Intratropical migrant with a breeding population in Los Tuxtlas. Present from 21 Mar. in spring; last autumn date observed was 4 Sept. Loetscher (1941) considered that nearly all were gone from Veracruz after Aug. Females showed breeding evidence in mid-Apr. (distended oviduct 13 Apr., egg in oviduct 15 Apr.).

Green Shrike-Vireo (*Vireolanius pulchellus*). Although Andrle (1967) considered the species rare, we found it to be FC in rainforest and oak-sweetgum canopy near El Bastonal (Jan.–Mar.) and on Volcán Santa Martha (Mar.). As Loetscher (1941) noted, individuals are usually detected by their calls. Phillips (1991) named the Los Tuxtlas population *V. p. ramosi.*

Golden-winged Warbler (*Vermivora chrysoptera*). To Andrle's (1966) two spring (18, 19 Apr.) and one autumn (23 Sept.) records we add our five specimens taken 26 Sept., 19, 21 Apr., and 6, 12 May.

Tennessee Warbler (*V. peregrina*). Andrle (1966) listed this species as a rather uncommon migrant. We have capture or specimen records of 64 individuals 4 Oct.–13 Nov., 19, 26 Mar., 29, 30 Apr., and 5, 31 May, and numerous sightings from 19 Sept. to 12 Dec. In addition, there seemed to be an influx of migrants during 13–19 Apr. 1975. This species is a common migrant in spring and autumn in Veracruz, as suggested originally by Miller et al. (1957). Most birds were found in 1–5 yr-old second-growth, or in large fruiting *Ficus* sp. trees at the edge of rainforest, although the La Peninsula (five) and Volcán Santa Martha (one) captures were in primary rainforest.

Nashville Warbler (*V. ruficapilla*). Not commented upon by Andrle (1966), and Loetscher (1955) noted no winter records. We observed individuals on 2 Dec., 2 Jan., and 16 and 18 Feb., suggesting wintering in low numbers.

Chestnut-sided Warbler (*Dendroica pensylvanica*). Andrle (1966) listed three spring and one autumn records. We have two autumn records (24 and 25 Sept.), and 40 spring records (18 Apr.–31 May). In addition, our observations suggest regular wintering. We have two specimens from 24 Dec. 1984 and 20 Feb. 1985, and about 24 sightings spanning the winter period: 2 Dec.–first week of Mar. This species was found in primary rainforest, where it did not show evidence of territoriality, as it does in Panamá (Greenberg 1984).

Cape May Warbler (*D. tigrina*). One specimen (7 Oct.) and two sightings

(three birds on 7 Oct., one on 10 Feb.) supplement the single previous Veracruz record, a sighting by Andrle (1966) on 20 Mar. 1960.

Black-throated Blue Warbler (*D. caerulescens*). NR. Our two specimens (21 Oct. and 1 Nov.) and four sight records (17 and 29 Nov., 21 and 25 Mar.) are the first verified records for Veracruz. Habitats included dense second-growth and the edge of disturbed rainforest.

Blackburnian Warbler (*D. fusca*). Our 13 specimens, collected between 10 and 27 May 1975, plus additional observations (24 Sept., 27 Oct., 1, 9, 10, 14, and 31 May) indicate that this species is considerably more common than suggested by the three earlier Veracruz records of Andrle (1966). Habitats ranged from moderately dense to rather open second-growth of variable heights.

Prairie Warbler (*D. discolor*). NR. The first verified records for Veracruz are specimens taken 30 Oct., 1 and 15 Jan., and 12 Feb. These plus an additional sighting on 30 Oct. were in clumps of second-growth consisting mainly of *Solanum* sp.

Palm Warbler (*D. palmarum*). Although listed for Veracruz on questionable grounds by Davis (1972), we collected three specimens (two on 23 Nov. 1974 and one on 7 Jan. 1974). All three were foraging in heavily grazed pastures with sparse clumps of *Solanum* sp. 1+ m in height, and areas of bare soil. The specimens were identified by A. R. Phillips as *D. p. palmarum*. Individuals were seen on 9 and 10 Feb. 1983 and occasionally Jan.–Mar. at El Bastonal (all in heavily grazed pasture).

Bay-breasted Warbler (*D. castanea*). NR. Not reported for Veracruz by Loetscher (1941, 1955) or for Los Tuxtlas by Andrle (1966), this species migrates through Los Tuxtlas and is probably more common in spring than autumn. We have records from Oct. (one specimen, two sightings), Nov. (one specimen, five sightings) and May (22 individuals captured or collected, 13 sightings). The birds were found mostly in second-growth consisting of tall shrubs and short, 3–10 m trees, or in fruiting *Ficus* sp. trees at the edge of rainforest.

Cerulean Warbler (*D. cerulea*). Our three specimens (one on 13 and two on 16 Apr.) and one sighting (1 May) add to the three previous records for Veracruz (all spring), and agree with Andrle's (1966) statement that the species is a rare migrant. They were found along forest edge.

Prothonotary Warbler (*Protonotaria citrea*). The 5–6 autumn records cited by Andrle (1966) apparently are the only previous records for Veracruz. We collected seven specimens and observed 16 other birds 11 Aug.–16 Oct., and captured one bird at La Peninsula on 30 Mar. (apparently the only spring record). Most of these birds were at the edge of disturbed rainforest in dense secondary vegetation. Foraging birds were seen as high as 15 m in *Ficus* sp. trees.

Swainson's Warbler (*Limnothlypis swainsonii*). NR. Our 18 specimens (ten from 20 Sept.–16 Oct.; two from 15 and 22 Jan.; two from 25 and 30 Mar.; and four from 6 and 7 Apr.) supplement the records of Loetscher (1941) and Peterson and Chalif (1973), who considered this species a casual to rare migrant and winter visitor along the Gulf coast. Birds were seen at the edge of disturbed rainforest in dense second-growth, typically foraging at less than 4 m.

Mourning Warbler (*Oporornis philadelphia*). Loetscher (1941, 1955) noted a general absence of autumn records of this species in Veracruz; we have one specimen from 4 Oct. and note another taken by R. W. Dickerman on 10 Oct. 1956 near Martinez de la Torre. In Los Tuxtlas this species was more common in spring (14 records, 29 Apr.–24 May).

MacGillivray's Warbler (*O. tolmiei*). Andrle (1966) noted only autumn records; all five of our specimens are from spring (8–13 May).

Canada Warbler (*Wilsonia canadensis*). Although Andrle (1966) considered this species to be an uncommon spring and autumn migrant, we handled 183 individuals between 2 Sept.–12 Oct., and 25 Apr.–24 May. We also observed many others within these periods.

Fan-tailed Warbler (*Euthlypis lachrymosa*). NR*. Not reported by Andrle; seems very rare. We have one sighting on 20 Jan. 1983 at Playa Escondida during a *norte* (storm), and another of a singing male on 15 Mar. 1985 at about 500 m on Volcán Santa Martha.

Red-legged Honeycreeper (*Cyanerpes cyaneus*). Although Loetscher (1941), Andrle (1967), and the AOU (1983) considered this species to be resident, our evidence suggests that the population in Los Tuxtlas is migratory. It appears to be absent from Los Tuxtlas during much of the boreal winter (Dec.–mid-Mar.). We have 22 captures at La Peninsula in spring (6 Apr.–26 May), and no autumn captures. At the Station we have four autumn captures (25 Aug.–13 Oct.) with sightings from 5 Aug. to 25 Nov., and spring records from 26 Mar.–26 May. The lack of later spring records is due to our absence.

Blue-crowned Chlorophonia (*Chlorophonia occipitalis*). VR. Andrle (1967) reported it from 300 to 750+ m. We have four specimens (24 Feb. and 8 Jan. [three]) at elevations of 100 m and less. The Jan. birds were immature females feeding in a noisy flock of 15, about 12 m above the ground, in a *Ficus* sp. tree near the edge of disturbed rainforest. Other observations were made on 9 and 16 Jan. 1975, and 8 Jan. 1983.

Savannah Sparrow (*Passerculus sandwichensis*). NR. There appear to be few Veracruz records of this species (cf Wetmore 1943:338), although Loetscher (1955) thought that it was probably regular to locally common in winter. Three were taken on 2 Nov., 30 Mar., and 15 Apr. The bird taken on 2 Nov. was attracted to lights at night and was in migratory condition.

Clay-colored Sparrow (*Spizella pallida*). NR. Loetscher (1955) noted only a single record for Veracruz. We took one on 17 Oct. 1974, and had sightings of single birds on 7 and 11 Dec.

Lark Sparrow (*Chondestes grammacus*). NR. Appears to be uncommon in winter in Veracruz (Loetscher 1955, cf Wetmore 1943:338). Three were obtained on 4 Oct. and 1 and 5 Apr. One (female; 4 Oct.) was identified by A. R. Phillips as *C. g. strigatus.*

Grasshopper Sparrow (*Ammodramus savannarum*). NR. Only two previous specimens are recorded for Veracruz (Wetmore 1943:338, Brodkorb 1943:87). We took two on 4 and 21 Apr.

Dark-eyed Junco (*Junco hyemalis*). NR. An immature female, netted near the Station at the edge of a recently cleared field on 27 Nov. 1973 was identified by A. R. Phillips as *J. h. hyemalis.* This occurrence, which coincided with a recent *norte,* represents the first record of this species for Veracruz.

Eastern Meadowlark (*Sturnella magna*). VR. We found this species to be a fairly common but local species in moist grassy lowland pastures. Specimens include adults in breeding condition. A specimen examined by A. R. Phillips was identified as *S. m. mexicana.* A few of the songs heard at various times and places through the winter period suggested *S. neglecta.*

Brown-headed Cowbird (*Molothrus ater*). NR. A male and female collected near cattle in a closely grazed lowland pasture on 6 May 1975, and a sighting on 7 May 1975, provide the only records for Los Tuxtlas. By size, the two specimens seem to represent two races, the male (wing 101.5 mm) *M. a. obscurus,* and the female (wing 101.0 mm) either *M. a. ater* or *artemisiae.*

Hooded Oriole (*Icterus cucullatus*). VR. Four birds reported by R. W. Dickerman (in Andrle 1967) on 7 Aug. 1962 constitute the only previous records. An adult female was taken on 16 Mar. 1974, in an area of dry, 3 m dune shrubbery, approximately 3.5 km east of La Palma, and a male was seen there on 31 Oct. 1974.

Chestnut-headed Oropendola (*Psarocolius wagleri*). VR. Andrle (1967) cited two records for Los Tuxtlas. We collected six specimens in nonbreeding condition (15 Aug. [two], 28 Sept., 10 Dec. [two], 1 May), and encountered groups of two–40 at irregular intervals during most seasons, usually at the edge of mature forest near the Station.

DISCUSSION

We obtained new information on the occurrence and abundance of a large number of migrant and resident birds in the Sierra de Los Tuxtlas. Our results are primarily the product of a large-scale observation and collecting effort carried out over 18 months in a relatively small area.

Additional work in other areas of Los Tuxtlas suggested that the coastal situation of the initial survey was a primary reason for the relatively high number of new records. Species added in later work tended to be tropical resident, forest-related species, reflecting the habitats investigated (mostly primary rainforest). Few new migrant records were discovered in the 1980s.

Our findings are not surprising, given the numerous local microhabitats and the diversity of the resident and migratory avifauna. However, considerable effort preceded ours, including the impressive surveys of Andrle (1964, 1966, 1967). The intensity of earlier work might lead to the assumption that the occurrence and abundance of birds in Los Tuxtlas was well known. Thus, it is clear that caution should be used when interpreting avifaunal lists from areas that have not been the focus of intensive, long-term studies employing both observation and netting.

We recorded 58 species that appear to be new to Los Tuxtlas, or 14% of the total 405 species observed. Of these 58, 19 are probable local residents and the remaining 39 are temperate migrants (e.g., shorebirds, parulines) or vagrants (e.g., Brown Booby, Sooty Tern). Of these 58 noteworthy species, 40 are supported by voucher specimens. It is certain that these new records are a direct result of our sampling effort; mist netting documented the occurrence and abundance of hard-to-detect rainforest species, and collecting allowed accurate identification of morphologically similar species, such as *Empidonax* flycatchers. We do not find evidence in our study to support any type of "short-term avifaunal turnover." Rather, we conclude that the differences between our work and Andrle's are mainly a result of differences in sampling effort (or "pseudoturnover," see Lynch and Johnson 1974).

Rapid deforestation in the neotropics has undoubtedly had an impact on both resident and migratory birds. The recent increase of second-growth forests, woodlots, scrub, and pastures has resulted in an increase in the abundance of species dependent upon these habitats. On the other hand, of 328 bird species from the northern neotropics considered by Ramos (1985) to be in danger due to tropical forest destruction, 96 species (29%) occur in Los Tuxtlas. This total represents 23.7% of the 405 species we recorded. The impact of deforestation on these primarily resident, rainforest species can hopefully be monitored by comparing future surveys with our study.

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BREEDING BIOLOGY OF TRISTRAM'S STORM-PETREL ON LAYSAN ISLAND

JEFFREY S. MARKS AND SHAWNE M. LEASURE[1]

ABSTRACT.—Breeding biology of Tristram's Storm-Petrels (*Oceanodroma tristrami*) was studied on Laysan Island in the Northwestern Hawaiian Islands from 3 February to 14 June 1991. Adults arrived on Laysan from mid-October to November. Most egg laying occurred in December and January and hatching in February and March. The young fledged from late April to early June at 85–92 days of age. Their growth rate was best described by the logistic curve. Adults did not begin molt of remiges until after the breeding season. Eggs hatched at only nine of 27 nests (33%) found during incubation; five of these hatchlings fledged (56%). Abandonment rates were identical at nests where we handled adults and where we inspected eggs without handling adults. Because unattended eggs were destroyed quickly by Laysan Finches (*Telespiza cantans*), we suggest that Tristram's Storm-Petrels that co-occur with finches seldom neglect their eggs as is common among other species of storm-petrels. Modifications caused by reaching into a burrow (e.g., widening the entrance and dislodging soil from burrow walls) may be perceived by adult storm-petrels as a signal that the burrow may collapse. *Received 17 Dec. 1991, accepted 1 April 1992.*

Tristram's Storm-Petrel (*Oceanodroma tristrami*) is one of the least known of the northern hemisphere storm-petrels. Its range is restricted to the western and central North Pacific Ocean, with the largest numbers (perhaps 2000–4000 pairs) occurring on Nihoa, Laysan, and Pearl and Hermes Reef in the Northwestern Hawaiian Islands (Rauzon et al. 1985, Harrison 1990). Smaller numbers nest on the Izu and Volcano islands of Japan. The pelagic distribution of Tristram's Storm-Petrel is thought to be confined to waters near and north of the breeding islands and to the expanse of ocean between Hawaii and Japan (Crossin 1974, AOU 1983, Harrison 1987). Because it nests in winter when access to remote islands is difficult, little is known about its breeding biology. Indeed, virtually all published accounts of Tristram's Storm-Petrel in Hawaii are based on brief visits to breeding islands (e.g., Ely and Clapp 1973, Amerson et al. 1974, Crossin 1974, Rauzon et al. 1985) or on inferences drawn from other species of hydrobatids (viz Harrison 1990).

In this paper, we describe aspects of the breeding biology of Tristram's Storm-Petrel on Laysan Island in the Northwestern Hawaiian Islands. We also discuss how an endemic egg predator, the Laysan Finch (*Telespiza cantans*), may influence nesting success and incubation behavior of adults. Lastly, we present a hypothesis as to why incubating storm-petrels are so sensitive to human disturbance.

[1] Cooperative Wildlife Research Unit, Univ. of Montana, Missoula, Montana 59812.

STUDY AREA AND METHODS

Laysan Island (25°46′N, 171°44′W) is a low (elevation <12 m) coral island located about 1500 km WNW of Honolulu, Hawaii. The island has an area of 397 ha, including a 70-ha hypersaline lake. Laysan Island is part of the Hawaiian Islands National Wildlife Refuge and is uninhabited except when researchers are present. Approximately 47% of the island is vegetated (Morin and Conant 1990). The most abundant plant is a native bunchgrass (*Eragrostis variabilis*). Ely and Clapp (1973) and Morin and Conant (1990) provide a more detailed description of the island, including a complete list of plants. From late winter to early spring 1991, Laysan was mostly windy (often 20–30 knots) and dry (<6 cm of rain in February and March); temperatures ranged from 14–25°C in February, 16–27°C in March, and 19–30°C in April and May (J. S. Marks, unpubl. data).

Marks noted autumn arrivals of storm-petrels in 1988 and 1990. In 1991, we visited Laysan from 3 February to 14 June; all observations of nesting storm-petrels occurred during this visit. We did not attempt to census the number of breeding storm-petrels on Laysan, and we monitored only a few of the nests there. Nests were located during daytime by searching for burrows on the ground surface and beneath clumps of *Eragrostis*.

Initially, we removed incubating adults from their burrows for about 5–8 min for banding, weighing, and measuring. After several nests failed (presumably from abandonment; see below), we inspected nests by removing eggs without handling the adults. Eggs were returned to incubating adults in 1–2 min. Eggs were checked every 2–5 days until they were starred and then every 1–2 days until hatching. Adults always remained in their burrows during egg checks and immediately settled upon their eggs when we returned the eggs to the burrows.

We also caught adults at night on the ground surface. We measured body mass (± 1 g using a 100- or 300-g Pesola spring balance), wing chord (± 1 mm using a stopped ruler), exposed culmen length (± 0.1 mm), tarsus length (± 0.1 mm), and scored molt of flight feathers for 80 adults caught during February. Adults caught in April and May (N = 50) were weighed and inspected for molt but were not banded or measured.

Beginning the day after hatching, nestlings were weighed (± 1 g) every seven days between 14:00 and 17:00 h HST. We fitted nestling mass data to three sigmoid growth models (logistic, Gompertz, and von Bertalanffy) using nonlinear least squares regression (SYSTAT NONLIN; Wilkinson 1986) and estimated growth parameters (i.e., the growth constant K, asymptotic mass, and initial mass) from the model that yielded the lowest residual mean square error (Ricklefs 1983). We also calculated t_{10-90}, which is the amount of time required to grow from 10 to 90% of the asymptotic mass (Ricklefs 1967).

Adult vocalizations were recorded with a Marantz PMD 201 cassette recorder (tape speed 4.75 cm sec^{-1}) and a parabolic microphone. Recordings were made of birds vocalizing from inside burrows or from the ground surface. Sonograms were prepared on a computer using MacRecorder software.

Statistical tests (two-tailed) were based on Zar (1984); data were log-transformed when appropriate. Differences were considered significant as $P \leq 0.05$.

RESULTS

Timing of breeding and adult attendance at nest colonies.—Adults arrived at and departed from the island only at night. In 1988 and 1990, adults were first heard on the island on 10 and 15 October, respectively, and were numerous by mid-November. Adults had not arrived when Marks left Laysan on 8 September 1989. Most (if not all) of the eggs had been laid by the time we arrived in early February 1991. Several nestlings

found between 5 and 10 February were ≤one week old. We documented hatching dates at nine nests. Four chicks hatched between 10 and 14 February, three between 22 and 26 February, and one each on 2 and 15 March. Assuming an incubation period of about 45 days (the actual period is unknown), most of the eggs would have been laid in December and January. Eggs were starred for ≥3–7 days before hatching. Adults attended hatchlings at the nine nests where eggs hatched but were absent at three nests on the day after hatching. Two of these chicks subsequently fledged. Apparently, adults brood nestlings during daytime for no more than 2–3 days after hatching. We did not check nests at night.

Hundreds of adults attended nesting colonies at night during February and March. Many of these birds were nonbreeders that vocalized singly or in pairs from burrows or the ground surface. Adult numbers declined sharply during late April. On 5 May, we found only 13 adults after searching the densest nesting areas for 5 h. Most of the adults that bred successfully probably deserted their chicks between mid-April and mid-May. Most fledglings left the island between mid-April and late May. The latest known departure of a fledgling was 11 June.

Nest and egg characteristics.—Storm-petrel nesting activity was confined to the band of mixed vegetation (*Eragrostis variabilis, Ipomoea pescaprae,* and *Sicyos* sp.) that extended for about 50–250 m around the perimeter of the lake basin in the center of the island. We found 31 burrows with eggs between 5 February and 10 March. Ten were beneath live clumps of *Eragrostis,* eight beneath residual clumps of *Eragrostis,* six among *Ipomoea* or *Sicyos,* and seven in bare sand near vegetation. Burrows were about 8–10 cm in diameter at the entrance and ranged from 20 cm to at least 80 cm in length (i.e., the maximum length we could reach).

Eggs were white and often had a faint ring of tiny red spots near the blunt end (but see Rauzon et al. 1985). Thirty eggs had a mean length (L) of 3.88 cm ± 0.16 (SD; range = 3.48–4.28) and a mean breadth (B) of 2.80 cm ± 0.13 (range = 2.52–3.17). Egg volumes ($V = 0.507LB^2$; Hoyt 1979) ranged from 11.2 to 21.8 cm^3. These egg measurements are similar to those of Rauzon et al.'s (1985) nine eggs measured on Laysan in 1981.

Nesting success, effects of researcher disturbance, and egg predation by finches.—Eggs hatched at only nine of the 27 nests (33%) found during incubation (excluding nests in four burrows that we stepped on by accident). One chick died while hatching, two chicks died within 14 days after hatching, and one 72-day-old chick disappeared after losing 21 g in a week. The remaining five chicks fledged, for an overall success rate of only 18%. Of the 22 nests that failed during incubation, 12 failed between our first and second visits and five between our second and third visits. This suggests that most of the nest failures during incubation were due

to abandonment in response to our nest visits. Nest abandonments must have occurred at night, because adults never left their burrows during daytime and always returned to their eggs immediately after we released them back into their burrows. The failure rate during incubation was identical (66.7%) at the 18 nests where we handled an adult and at the nine nests where we inspected eggs without handling an adult. Thus, the rate of abandonment was independent of whether we handled adults at their burrows.

Broken eggshells in or near burrows indicated that Laysan Finches destroyed the eggs in all but two of the failures that occurred during incubation. We saw Laysan Finches investigating Tristram's Storm-Petrel and Bonin Petrel (*Pterodroma hypoleuca*) burrows on numerous occasions in February and March. Laysan Finches are well-known predators of seabird eggs (Fisher 1903, Bailey 1956, Ely and Clapp 1973), and this behavior was more prevalent during winter than at any other time of year (J. S. Marks, pers. obs.). Especially during winter, finches probably know the status of most (if not all) of the petrel burrows within their home ranges. Unattended Tristram's Storm-Petrel eggs (at least in burrows <80 cm in length) are probably detected and consumed by Laysan Finches within a day or two of becoming available.

Adult morphology and flight feather molt.—The mean body mass of adults was 92.0 g in February (SD = 8.2, range = 71–112, N = 80), 85.5 g in early April (SD = 5.8, range = 77–97, N = 30), and 83.4 g in early May (SD = 11.2, range = 70–104, N = 20). Body mass differed significantly among months (ANOVA, $F = 12.64$, df = 2,127; $P < 0.0005$; data log-transformed). Storm-petrels were heavier in February than in April or May (Tukey test, $P < 0.05$). Rauzon et al. (1985) also noted a decline in body mass of adult Tristram's Storm-Petrels from winter to spring. Means for the other measurements of the 80 adults caught in February were: wing chord, 179.9 mm (SD = 3.9, range = 172–192); exposed culmen, 18.2 mm (SD = 0.6, range = 16.8–19.5); and tarsus length, 28.4 mm (SD = 0.9, range = 26.4–30.6). Our measurements were similar to those of Rauzon et al. (1985) except for tarsus length, which averaged 2 mm longer ($t = 7.22$, df = 101, $P < 0.0005$). This difference was due to Rauzon et al. (1985) measuring to the distal end of the tibiotarsus rather than to the proximal end of the tarsometatarsus (M. J. Rauzon, pers. comm.).

Adults had fresh-looking primaries in February, and we found no indication that they began molting remiges during the breeding season (N = 130 adults inspected between February and early May). Four adults (all apparent nonbreeders) were molting from 1–3 retrices on one side of the tail between 14 and 25 February. Thus, most adults begin molting their flight feathers at sea after the breeding season. We did not check for molt during autumn when the adults first arrived on Laysan.

Encounters with banded adults.—We caught two storm-petrels that had been banded previously on Laysan. The first, caught on 22 February 1991, was at least three years old when banded on 16 November 1980. The numbers on its aluminum band required chemical etching to be legible. At a minimum age of 14 years, this bird is the oldest known Tristram's Storm-Petrel (previous record was 9 years; Clapp et al. 1982). The second, caught on 28 February 1991, had been banded after its second year on 10 April 1987. Its incoloy band was unworn. Including the two birds noted above, 27 Tristram's Storm-Petrels banded as adults have been recovered in Hawaii, each on the same island at which it was banded (Bird Banding Laboratory, unpubl. data). None of the Tristram's Storm-Petrels banded as nestlings has been recovered.

Nestling development and growth.—Like all hydrobatids, Tristram's Storm-Petrels hatched covered with down and with their eyes closed. The absence of adults at nests soon after hatching suggests that nestlings could thermoregulate at 2–3 days old. The egg tooth disappeared and the eyes opened between days 8 and 15. Mass increased rapidly for five weeks until nestlings reached 121–155% of the average adult mass for February (Fig. 1). Mass remained relatively constant from weeks five to 11 and then dropped to adult mass in the two weeks before fledging (Fig. 1). The five nestlings that we followed from hatching to fledging left the nest at a mean age of 89.2 days (SD = 3.1, range = 85–92) and a mean mass of 93.6 g (SD = 4.0, range = 88–99). Only one nestling gained mass after day 78, suggesting that adults seldom fed their young during the two weeks before fledging. The remiges erupted between days 30 and 35, and the primaries were still in sheath in four of five fledglings. The exception had fully grown primaries on day 90. Fledglings had trace amounts of down or no down adhering to their contour feathers.

Nestling masses obtained after day 78 (when mass began to decline) were excluded from the growth curve analyses. All three growth models provided reasonable parameter estimates (Table 1). The logistic curve yielded the lowest residual mean square error, followed by the Gompertz and the von Bertalanffy curves. The parameter estimates were nearly identical whether derived from the average masses of the five nestlings that fledged or from the average masses of all nestlings of known age (including three that did not fledge). Data presented in Table 1 were derived from the larger sample of nestlings. Growth of individual nestlings that survived to fledging was best described by the logistic curve in three cases and by the von Bertalanffy curve in two cases. On average, nestlings required about 44 days to grow from 10 to 90% of the asymptotic mass (Table 1).

Adult vocalizations.—Tristram's Storm-Petrels produced two main vocalizations, the flight call and the burrow call (Fig. 2). Flight calls were

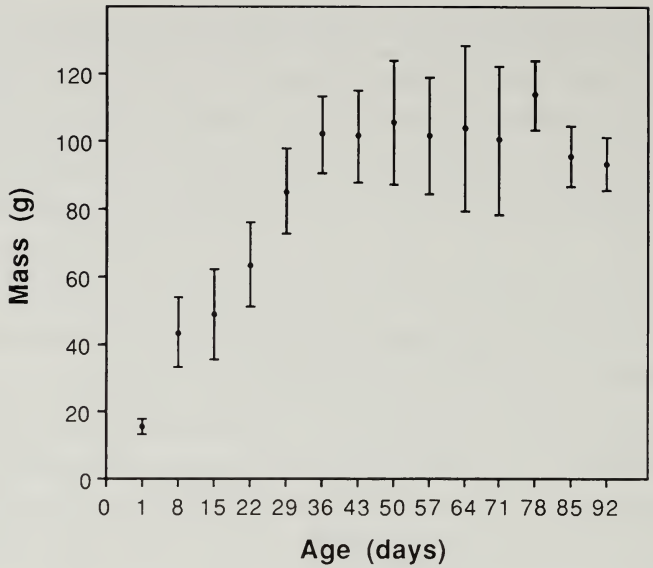

FIG. 1. Average body mass (± SD) of Tristram's Storm-Petrel nestlings on Laysan Island, February to June 1991. Samples sizes are 8 (day 1), 7 (day 8), 6 (days 15–71), 5 (days 78–85), and 2 (day 92).

given in flight, on the ground, and in burrows. They consisted of 6–7 syllables of fundamental frequency bands and their overtones (Fig. 2). Burrow calls were given from inside burrows or on the ground but not in flight. They consisted of series of repeated notes that often lasted for >one min. They are similar to the burrow calls of Swinhoe's Storm-Petrel (*Oceanodroma monorhis*) depicted by Taoka et al. (1989b).

Recent studies have revealed sexual dimorphism in the vocalizations of five species of storm-petrels (Simons 1981; James 1984; James and

TABLE 1

PARAMETER ESTIMATES (± SE) OF THREE SIGMOID CURVES DESCRIBING GROWTH OF TRISTRAM'S STORM-PETREL NESTLINGS ON LAYSAN ISLAND[a]

Growth model[b]	Growth rate	Asymptotic mass (g)	Initial mass (g)	t_{10-90} (days)
Logistic	0.100 ± 0.012	107.1 ± 2.9	18.4 ± 2.3	43.9
Gompertz	0.070 ± 0.011	109.2 ± 4.7	15.1 ± 4.7	44.1
von Bertalanffy	0.060 ± 0.008	110.3 ± 3.8	20.0 ± 1.8	45.7

[a] Analyses based on data in Fig. 1 to 78 days of age.
[b] The logistic model yielded the lowest residual mean square error; $r^2 = 0.97$.

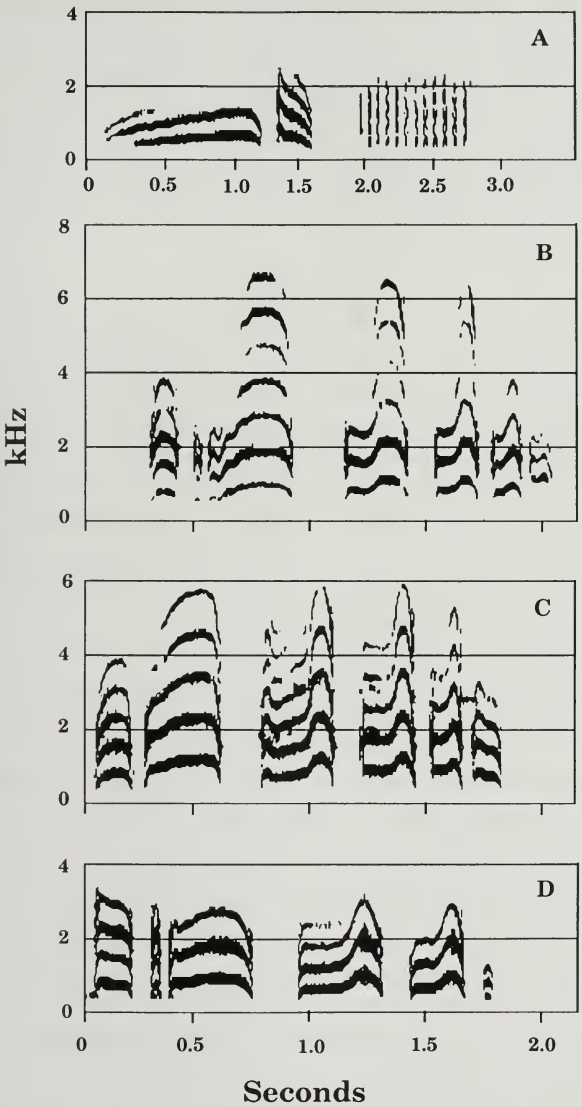

FIG. 2. Sonograms of four adult Tristram's Storm-Petrels on Laysan Island, February 1991: burrow call (A), and flight calls (B–D). The sex of the birds was not known.

Robertson 1985a; Taoka et al. 1989a, b). We could not sex birds by cloacal inspection because we arrived after egg laying, and we did not perform laparotomies. Moreover, we recorded the vocalizations of only a small number of individuals. Thus, we did not determine whether the sex of Tristram's Storm-Petrels can be distinguished by voice. Because procellariiforms that call in flight tend to have sex-specific calls (James and Robertson 1985b), Tristram's Storm-Petrels are good candidates for further research into this phenomenon.

DISCUSSION

Tristram's Storm-Petrels are similar to most other hydrobatids in that they are strictly nocturnal on land, they nest in burrows on remote islands, and they abandon their egg readily when disturbed by humans. Timing of molt is similar to that of other tropical species (Band-rumped Storm-Petrel [*Oceanodroma castro*] and Wedge-rumped Storm-Petrel [*O. tethys*]) that do not overlap flight feather molt with the breeding period (Harris 1969, Ainley et al. 1976). Being among the largest of the storm-petrels (Harrison 1987), they lay a larger egg and have a longer nestling period than other species for which data are readily available (Table 2). Harrison's (1990:141) statement that the young fledge in 58–72 days was based on speculation and is incorrect. Rauzon et al.'s (1985) report of "fully-feathered chicks" on Nihoa Island in February suggests that egg laying would have occurred in the first half of October—an extremely early date for this species. Visits to breeding islands from October through January are needed to understand fully the timing of laying and to determine the length of the incubation period in Tristram's Storm-Petrel.

Nest abandonment, egg neglect, and the potential effect of egg predators on storm-petrel incubation behavior.—Storm-petrels often abandon their eggs following disturbance by researchers (e.g., Davis 1957a, Allan 1962, Ainley et al. 1974, Morse and Buchheister 1979, Boersma et al. 1980). Although abandonment is usually permanent, Boersma et al. (1980) observed adult Fork-tailed Storm-Petrels (*Oceanodroma furcata*) return to eggs 18 and 23 days after abandonment. The poor hatching success (33%) of Tristram's Storm-Petrels on Laysan probably resulted from Laysan Finch predation on abandoned eggs. It is also possible that eggs were destroyed by conspecifics as suggested for Band-rumped and Wedge-rumped storm-petrels (Allan 1962, Harris 1969). However, we never found storm-petrels occupying burrows after nest failures, and suitable nesting sites were not in short supply. Moreover, we routinely saw finches going in and out of nesting burrows; presumably, they were searching for unattended eggs to eat.

Storm-petrels (and many other procellariiforms) are also well-known

TABLE 2
COMPARATIVE DATA ON ADULT MASS, EGG SIZE, AND LENGTH OF NESTLING PERIOD IN STORM-PETRELS

Species	Adult mass (g)	Egg size (mm)	Nestling period (days)	Source[a]
Wilson's Storm-Petrel (*Oceanites oceanicus*)	37.6	33.4 × 24.2	60	1, 2
Black-bellied Storm-Petrel (*Fregetta tropica*)	57.5	37.0 × 27.0	68	3
British Storm-Petrel (*Hydrobates pelagicus*)	28.0	28.0 × 21.0	56–73	4, 5
Fork-tailed Storm-Petrel (*Oceanodroma furcata*)	59.2	34.6 × 26.3	51–66	6, 7
Leach's Storm-Petrel (*O. leucorhoa*)	41.9	33.0 × 24.0	59–70	5, 8, 9
Ashy Storm-Petrel (*O. homochroa*)	39.6	28.7 × 21.8	76	8, 10
Band-rumped Storm-Petrel (*O. castro*)	43.5	31.3 × 23.1	64–78	11, 12
Wedge-rumped Storm-Petrel (*O. tethys*)	25.8	27.8 × 20.6	?	12
Tristram's Storm-Petrel (*O. tristrami*)	92.0	38.8 × 28.0	85–92	13

[a] 1 = Beck and Brown (1972); 2 = Roberts (1940); 3 = Beck and Brown (1971); 4 = Davis (1957b); 5 = Cramp (1977); 6 = Boersma et al. (1980); 7 = Simons (1981); 8 = Ainley et al. (1974); 9 = Vermeer et al. (1988); 10 = Dawson (1923); 11 = Allan (1962); 12 = Harris (1969); 13 = this study.

for neglecting their eggs (Richdale 1965, Wilbur 1969, Pefaur 1974, Boersma and Wheelwright 1979). Egg neglect, as distinguished from abandonment, is an adaptive response to the temporary failure of a foraging bird to relieve its mate at the nest. Storm-petrel embryos tolerate chilling, and eggs may hatch after at least seven days of continuous neglect (e.g., Fork-tailed Storm-Petrel; Boersma and Wheelwright 1979). Five other species of storm-petrels are known to neglect their eggs for 1–5 days (reviewed by Pefaur [1974] and Boersma and Wheelwright [1979]). This behavior is probably widespread among hydrobatids.

Distinguishing abandonment from egg neglect can be difficult. Because most of the failures during incubation occurred soon after we visited a nest, we have assumed that the adults abandoned their nests. If we are correct, then Tristram's Storm-Petrels are highly sensitive to human disturbance. Nests in which we inspected eggs without handling adults had the same high failure rate as nests in which we banded and measured adults. Alternatively, some of the failures we observed may have begun as egg neglect rather than abandonment. Regardless of whether eggs were neglected or abandoned, however, the important point is that unattended

storm-petrel eggs on Laysan probably had little chance of hatching owing to predation by finches.

In this regard, a behavior that normally is adaptive in storm-petrels (viz egg neglect) would be selected against wherever storm-petrels and egg predators co-occur. Thus, we predict that Tristram's Storm-Petrels seldom neglect their eggs on Laysan and Nihoa islands, both of which have large numbers of endemic egg-eating finches (the Nihoa Finch [*Telespiza ultima*] is an egg predator; J. S. Marks, pers. obs.). In 1967, Laysan Finches were introduced intentionally on Pearl and Hermes Reef (Conant 1988), which is the only other location in Hawaii with large numbers of Tristram's Storm-Petrels. Thus, a management effort on behalf of finches may have unwittingly reduced the nesting success of storm-petrels (see Conant 1988).

Future studies of Tristram's Storm-Petrel in Hawaii should determine the influence of finches on the nesting success and incubation constancy of storm-petrels and develop means of monitoring storm-petrel nests without causing high rates of abandonment. Such studies should include storm-petrel nesting islands that do not have finches (e.g., Necker Island and French Frigate Shoals).

Why are storm-petrels so sensitive to human disturbance?—We found no explanation in the literature for why human disturbance causes storm-petrels to abandon their eggs so readily. One reason might be that storm-petrels perceive humans to be predators and abandon their nests to avoid predation (P. D. Boersma, pers. comm.). Although this explanation is reasonable for areas where storm-petrels historically co-occurred with predators (including humans), it might not apply to areas like the Northwestern Hawaiian Islands where storm-petrels nest in the absence of predators, thus having no reason to perceive humans as predators. Moreover, if Tristram's Storm-Petrels abandoned nests to avoid "predation" by us, then they should have left their nests soon after we released the birds into their burrows. Instead, they returned to their eggs, and they must not have abandoned their nests until many hours after the disturbance.

We suggest that in some cases, the tendency to abandon a nest is related to nesting in burrows. At least in the sandy substrates common to the Northwestern Hawaiian Islands, burrows collapse occasionally (see also Stokes and Boersma 1991). We have found Bonin Petrels and Wedge-tailed Shearwaters (*Puffinus pacificus*) trapped in burrow cave-ins during each of five trips to Laysan since 1988. We suspect that Tristram's Storm-Petrels are similarly vulnerable. Perhaps storm-petrels perceive disturbance as a indication that the burrow is unsound and thus prone to collapse. Storm-petrel burrow entrances are small, and it is difficult to reach into a burrow without altering it (e.g., widening the entrance and

dislodging small amounts of soil from the ceiling and sides). Once they discover the disturbance, storm-petrels may respond by abandoning the burrow. Because storm-petrels are long-lived (≥31 years for Leach's Storm-Petrel [*O. leucorhoa*], Klimkiewicz and Futcher 1989), they might be expected to abandon reproductive attempts when faced with the risk of reduced life expectancy (Williams 1966, Goodman 1974). For storm-petrels that nest in sandy substrates, the collapse of a burrow may be just such a risk. For this hypothesis to be valid, abandonment should be uncommon in substrates that are unlikely to collapse. Data from the Galapagos Islands support this view; nest abandonment by Band-rumped and Wedge-rumped storm-petrels following human disturbance is rare (Harris 1969), and the birds nest in holes in lava rock that would be unlikely to collapse. Additional studies are needed to evaluate more fully the relationship between abandonment and nesting substrate in storm-petrels and other burrow-nesting procellariiforms.

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NOTICE TO INDIVIDUALS CONDUCTING RESEARCH IN THE NORTH PACIFIC

Because of a drastic population decline, the Steller sea lion has been listed as a threatened species under the Endangered Species Act. To reduce human disturbance, the National Marine Fisheries Service (NMFS) has placed restrictions on land and water approach in the vicinity of Steller sea lion rookeries in the Bering Sea, Aleutian Islands, and Gulf of Alaska. These prohibitions apply to all individuals and activities unless specifically exempted by NMFS. For further information regarding Steller sea lion regulations, contact NMFS, Protected Resources Management Division, P.O. Box 21668, Juneau, Alaska 99802 (907) 586-7235.

Wilson Bull., 104(4), 1992, pp. 732–738

SHORT COMMUNICATIONS

Avian characteristics of an urban riparian strip corridor.—Riparian strip corridors bordered by agricultural fields and forest clear-cuts have a distinct, induced-edge habitat with greater density and diversity of birds and denser vegetation than large, contiguous forests (Ranney et al. 1981, Noss and Harris 1986, Temple 1986). No studies have determined if similar relationships exist for stream corridors in urban landscapes where habitat interfaces are different. The ability of urban corridors to maintain the ecological integrity of riparian systems is relatively unexplored (Adams and Dove 1989, Barrett and Bohlen 1991). This paper compares avian density, diversity, and richness of an urban stream corridor with that found along a stream system in a large rural habitat block.

Methods.—Our study was conducted on two areas in Alachua County, Florida: the urbanized Hogtown Creek and the rural San Felasco Hammock State Preserve. The predominant habitats in the Hogtown Creek corridor in western urbanized Gainesville are flatwoods and mesic hardwood hammocks. San Felasco is a 2500-ha preserve consisting mostly of mesic hardwood hammock and is located 8 km northwest of Gainesville. This park contains one of the largest undeveloped stands of mesic hammock in peninsular Florida. Study plots within the two study areas were located along the Hogtown Creek in 20–60 m wide (narrow) and 75–150 m wide (wide) naturally vegetated corridor segments. Criteria for selecting plots included (1) predominantly mesic hardwood hammock plant communities, (2) placed near streams with at least 20 m of natural forest vegetation width on one side, and (3) bordered on both sides by residential housing.

Potential control plots (San Felasco) were marked on a USGS topographical map within hardwood hammock communities along two creeks within the State Preserve at 150-m intervals. Of these, nine were selected randomly. No residential housing or man-made clearings were present within 500 m of control plots. Both study and control plots were circular with 50-m radii, and their centers were at least 150-m apart and 10 m from the edge of the creekbank. Study plots were located on the side that contained the widest area of natural forest, and control plots in San Felasco were randomly situated on either side of the creek. Six narrow and nine wide Hogtown plots and nine San Felasco plots were studied.

We sampled breeding birds from 23 April through 8 June in 1989 and 16 April through 31 May in 1990. Winter sampling was conducted from 13 December 1989 to 1 February 1990. During the breeding season of 1989, all plots were sampled six to nine times. Each plot was sampled eight times during the winter and breeding seasons of 1990. Sampling began at sunrise and ended approximately 3 h later on calm, clear mornings. Counts began at different plots each day to avoid time-of-day activity biases. After arriving at the plot a one-min equilibration period was followed immediately by an eight-min sampling period to detect and record birds seen and heard (Reynolds et al. 1980). Observations were made from the center of each plot. No bird detected outside the 50-m radius plot was counted.

Average density of birds (all species combined) per sampling period, average frequency of birds (all species combined), and average density of each species per sampling period were determined. Richness was the number of species that occurred on the plot during the study season. We measured bird species diversity per plot by using Brillouin's index (Pielou 1966, Magurran 1988). This index is preferred over the Shannon Diversity index when the assumption of random sampling is violated (Pielou 1966, Magurran 1988). Because some species may be more detectable than others, random sampling was not assumed and no comparisons between species were made (Blake and Karr 1987).

Circular plots of 0.031 ha (20-m diameter) were centered on bird sampling plots for vegetation sampling during the summer of 1989. Vegetation data were collected (Table 1).

TABLE 1
HABITAT MEASUREMENTS

Height and species of all trees ≥3 cm dbh
Height class, species, and canopy cover estimate of all woody stems <3 cm dbh and >0.5 m tall within two perpendicular, 2-m-wide, 20-m-long, x-shaped transects
Number of all woody stems <3 cm dbh and <0.5 m tall within two perpendicular 2-m-wide, 20-m-long transects
Count of all vine stems or vine leaves that intersect the centerline of the two perpendicular transects
Estimation of vertical structural diversity by recording the presence or absence of vegetation at height intervals of 0–0.3 m, 0.31–5 m, 5.1–10 m, and >10 m

Diversity of shrubs and trees was calculated with the Shannon-Weaver formula, and evenness (E) = Shannon index/log of the cumulative number of species (Magurran 1988).

We measured the percent coverage of vegetation types (Myers and Ewel 1990), including hardwood hammock, pine flatwoods, and percent cleared area by examining color infrared vertical photographs of the Hogtown Creek at a scale of 1:15,840. All San Felasco plots were in hardwood hammock communities. A 20-ha circle was drawn to scale (2-cm radius) on transparent material, and its center was aligned with the center of the bird census plot on the photograph. Areas covered by various vegetation types were outlined on the transparency using a fine-point felt-tipped pen. The transparency was then placed over a dot grid of 16 dots per square cm. Dots within an outlined vegetation patch were counted, and a percent of the total for each vegetation type was calculated.

Housing density in the vicinity of the plots was measured on a map by drawing a scaled 3-ha circle around the center of each plot, then counting the number of houses within each circle. The percent cover of vegetation type, housing density, and width comprised the development variables. Housing density was zero in San Felasco.

We compared habitat characteristics among plots using the non-parametric Kruskal-Wallis test (Hollander and Wolfe 1973). When a significant treatment effect ($P \leq 0.05$) was found, a non-parametric multiple-comparison test for unequal sample sizes was used to determine which treatments differed ($Q > 2.394$, $P \leq 0.05$; Hollander and Wolfe 1973, Zar 1984). We used the SAS multiple regression procedure (SAS Institute Inc. 1988) to determine which habitat variables explained most of the variation in bird community parameters and species densities. Any two variables that were highly and significantly correlated ($r \geq 0.70$, $P \leq 0.05$) were not used in the same regression model. The variable that produced a significant model with the highest r^2 was kept. No model included more than five independent variables.

We compared five bird community parameters and densities of 22 bird species among treatments with the Kruskal-Wallis test. When a significant treatment effect ($P \leq 0.05$) was found, a non-parametric multiple-comparison test for unequal sample sizes was used to determine which treatments differed ($Q > 2.394$, $P \leq 0.05$). To eliminate species that had a low frequency of occurrence, only those that were observed in at least 50% of the plots of any one treatment were tested. Before conducting the correlation and multiple linear regression analyses, variables were transformed to achieve normality using the Box-Cox transformation technique (Sokal and Rohlf 1981). The two Hogtown treatments were pooled for these analyses because only one significant difference in a species' density was found when tested separately.

TABLE 2

AVERAGES OF BIRD COMMUNITY PARAMETERS ALONG THE HOGTOWN CREEK AND IN SAN FELASCO HAMMOCK STATE PRESERVE, IN ALACHUA COUNTY FLORIDA, DURING 1989 AND 1990[a]

Variable	Treatment		
	Narrow	Wide	San Felasco
Spring			
Bird density	0.76 a	0.75 a	0.51 b
Bird species richness	11.91 a,b	10.66 a	12.66 b
Bird species diversity	0.77 a	0.74 a	0.87 b
Evenness	0.65 a	0.67 a	0.83 b
Bird frequency	0.39 a	0.37 a	0.33 a
Winter			
Bird density	0.78 a	0.76 a	0.44 b
Bird species richness	13.33 a	11.55 a	10.00 a
Bird species diversity	0.83 a	0.76 a	0.77 a
Evenness	0.64 a,b	0.63 a	0.74 b
Bird frequency	0.30 a,b	0.31 a	0.22 b

[a] Kruskal-Wallis multiple-comparison test for unequal sample sizes was used to determine differences. Values with identical letters were not significantly different from each other.

Results.—We detected fifty-three bird species. During spring, average density of birds was greater and bird species diversity and evenness were less in Hogtown Creek plots than in San Felasco (Table 2). Of nine resident species, five (American Crow [*Corvus brachyrhynchos*], Blue Jay [*Cyanocitta cristata*], Carolina Wren [*Thryothorus ludovicianus*], Northern Cardinal [*Cardinalis cardinalis*], and Red-bellied Woodpecker [*Melanerpes carolinus*]) had higher densities in one or both Hogtown Creek treatments than in San Felasco. One resident (Pileated Woodpecker [*Dryocopus pileatus*]) was more common in San Felasco than in wide plots (K-W test; $Q = 2.531$, $P = 0.04$). Of seven neotropical migrants, four (Acadian Flycatcher [*Empidonax virescens*], Hooded Warbler [*Wilsonia citrina*], Red-eyes Vireo [*Vireo olivaceus*], and Summer Tanager [*Piranga rubra*]) had higher densities in San Felasco. Acadian Flycatchers and Hooded Warblers were not detected in narrow plots, and Summer Tanagers were not detected in any plots along the Hogtown Creek.

During winter, bird density was greater in both Hogtown Creek plots compared to San Felasco ($Q = 3.776$, $P = 0.005$ and $Q = 3.104$, $P < 0.001$; Table 2). Evenness was greater in San Felasco than in wide plots ($Q = 2.417$, $P = 0.05$), but not greater than in narrow plots. Bird species diversity did not differ among treatments. Four species had significantly different densities between treatments and eight did not. Blue Jays, Northern Cardinals, and American Robins (*Turdus migratorius*) had higher densities in one or both Hogtown Creek study plots than San Felasco. The Yellow-rumped Warbler (*Dendroica coronata*) had higher densities in narrow than in both wide ($Q = 2.408$, $P = 0.05$) and San Felasco plots ($Q = 2.623$, $P = 0.03$). This was the only species comparison where a difference was found between the two Hogtown Creek treatments.

Only four habitat variables differed among treatments. Tree height diversity was greater in San Felasco than in either narrow or wide plots ($Q = 3.19$, $P = 0.004$ and $Q = 3.458$, $P = 0.002$, respectively). Tree density was greater in San Felasco than in narrow plots ($Q = 2.807$, $P = 0.016$). Species richness of shrubs in narrow plots was greater than in San Felasco

($Q = 2.803$, $P = 0.016$). Vine density was greater in the narrow treatment vs San Felasco ($P = 0.038$). Of the 21 significant regression models using spring data, tree characteristics were included in six models for Hogtown Creek and seven for San Felasco. Shrub variables were included in five Hogtown Creek models and seven San Felasco models. At least one development variable (width and housing density) contributed to five models in Hogtown Creek. Average r^2 values were greater in San Felasco (0.9782 ± 0.1827 SD) than in Hogtown Creek (0.5611 ± 0.2071 SD; $t = 4.87$, df = 19, $P < 0.001$). Of the 15 significant regression models found using winter data, tree characteristics and hardwood hammock cover each were included in five Hogtown Creek linear regression models. Width contributed to four, whereas housing density and shrub characteristics were included in two models each. Tree variables contributed to all six models in San Felasco. Again, average r^2 values were greater in San Felasco (0.9592 ± 0.0307 SD) than Hogtown Creek (0.6585 ± 0.1382 SD; $t = 5.185$, df = 13, $P < 0.001$).

Discussion.—The three most obvious factors that might explain at least some of the avian differences between San Felasco and Hogtown are vegetation dissimilarities, width of the urban corridor, and adjacent land use.

Sunlight can penetrate the less dense Hogtown forest and allow shade-intolerant shrubs and vines to persist. Naturally caused fires that reduce understory vegetation also have been suppressed for several decades in the urban corridor. The implications of these relationships is that urbanization may indirectly influence avian differences by directly affecting their habitats. For example, the understory in the Hogtown may be too dense for species such as Hooded Warblers that nest and forage close to the ground. Other urban studies have established relationships between bird species richness, diversity, density, and composition and vegetation variables in urban residential areas (Woolfenden and Rohwer 1969, Geis 1974, Beissinger and Osborne 1982, Goldstein et al. 1986). However, no previous investigations have focused on urban corridors.

All five species (Acadian Flycatcher, Hooded Warbler, Pileated Woodpecker, Red-eyed Vireo, and Summer Tanager) that had higher densities in San Felasco are insectivorous and are known to be sensitive to the size of isolated forest islands (Whitcomb et al. 1981). For example, Robbins et al. (1989) found that the diameter of forest patches which had a 50% probability of occurrence for Acadian Flycatchers was 437 m, Red-eyed Vireo 178 m, Summer Tanager 713 m, and Pileated Woodpecker 1449 m. Tassone (1981) reported that Acadian Flycatchers and Pileated Woodpeckers occurred infrequently in riparian strips less than 50 m wide in clear-cut areas. Stauffer and Best (1980) found that the minimum forested riparian width in which Red-eyed Vireos were found in an agricultural landscape was 40 m.

In our study, Acadian Flycatchers and Hooded Warblers were not found in narrow corridor segments (≤60 m), and Summer Tanagers were not recorded throughout the Hogtown Creek (≤150 m). Our data provide more evidence to support the ecological phenomenon that some Neotropical migrants are sensitive to habitat areas and widths. It is reasonable to believe that these widths are related somehow to the diameter of the species' home range which varies in response to food supply, age of the individual, population density, and other factors.

The five resident species (American Crow, Blue Jay, Carolina Wren, Northern Cardinal, and Red-bellied Woodpecker) with higher densities in the Hogtown Creek than in San Felasco consist of omnivores (three species), insectivores (one species), and granivores (one species), feed on or close to the ground, are found commonly in edge habitat, and are considered to be insensitive to the size of forest interior. The two short-distance migrants with higher densities in Hogtown Creek in winter, the American Robin and Yellow-rumped Warbler, also are edge species (Whitcomb et al. 1981).

The lack of avian and habitat differences between narrow and wide plots compared to

the more frequent dissimilarities in these variables between the Hogtown and San Felasco suggests an inadequate range of widths studied. Although the ideal research design would include a larger continuum of sizes, local ordinances and development pressures tend to limit the variety of riparian widths available.

The importance of adjacent land use is illustrated by the fact that the development variables we measured were included in many significant regression models for the Hogtown Creek. Whitcomb et al. (1981) also found that the Acadian Flycatcher was more abundant in forests isolated by agricultural fields than those bordered by low-density suburban residential development. This suggests that the disturbance factors associated with residential housing may outweigh the habitat values of ornamental yard plantings. Several authors have reported that avian density and richness changes and fragment-sensitive forest species are replaced by edge species (Woolfenden and Rohwer 1969, Walcott 1974, Aldrich 1980, Beissinger and Osborne 1982, DeGraaf and Wentworth 1986, Gotfryd and Hansell 1986) in areas where natural forested habitats are replaced by mature suburbs.

Because the r^2 values for our Hogtown regression models were relatively low, we believe some unmeasured adjacent development variables were influencing bird-community parameters and individual-species' densities in this study area. There also may be a shift in importance from trees and shrubs in spring to development-associated variables in winter. Tilghman (1987) found that the density of adjacent buildings was one of four variables that accounted for much of the variation in bird species richness during winter in urban forest islands in Massachusetts. She speculated that the presence of bird feeders was responsible for this result.

As development continues to sprawl and alter natural landscapes, assessing impacts on local ecosystems becomes increasingly important. Habitat values of agricultural and urban landscapes must be taken into account to achieve regional goals of maintaining ecological integrity of natural systems (Schaefer et al. 1991). Lynch and Whitcomb (1978) reported that urban and suburban parks in the Washington, D.C. area failed as avifaunal preserves because from 1950 to 1970 many specialized, fragment-sensitive species were replaced by generalized residents.

At the local level, conservation strategies for forested riparian areas within urbanizing environments typically have been based only on flood control and water quality concerns (Zampella and Roman 1983, Barton et al. 1985, Budd et al. 1987). Consideration often is given to the recreational and educational opportunities they provide for local residents. Wildlife data such as presented in this paper also should be used to determine the consequences of various community greenspace options.

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RUTHE J. SMITH AND JOSEPH M. SCHAEFER, *Dept. Wildlife and Range Sciences, 118 Newins-Ziegler Hall, Univ. of Florida, Gainesville, Florida 32611-0430.* *Received 20 May 1991, accepted 20 April 1992.*

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The role of Marbled Murrelets in mixed-species feeding flocks in British Columbia.—Studies off the west coasts of Vancouver Island and the Queen Charlotte Islands indicate that Marbled Murrelets (*Brachyramphus marmoratus*) usually feed singly or in pairs (Carter 1984, Carter and Sealy 1990, Sealy 1973, 1975). Marbled Murrelets participated in mixed-species feeding flocks (Carter 1984; Carter and Sealy 1987, 1990; Chilton and Sealy 1987; Porter and Sealy 1981, 1982; Sealy 1973, 1975) but were not as prevalent as other species (Sealy 1973, Hoffman et al. 1981, Porter and Sealy 1981) and infrequently initiated the flock (Porter and Sealy 1982, Chilton and Sealy 1987). We describe events in a dense concentration of murrelets (Kaiser et al. 1991) in the more sheltered waters of the Strait of Georgia, east of Vancouver Island, where Marbled Murrelets were the major initiators and participants of mixed species feeding flocks.

Study area and methods.—The Okeover Inlet study area (50°5′N, 124°45′W) includes several small inlets and fiords on the southwestern coast of British Columbia (Fig. 1). It is sheltered from major Pacific storms by Vancouver Island and more locally by numerous small islands and peninsulas, creating a protected inshore habitat. The area is characterized by rugged, broken coastline, deep inlets and fiords and moderate tidal currents. Open sound, channel, inlet, and estuarine habitats were included within the study area. During the summer, the area had a resident population of about 370 Marbled Murrelets and 200 Glaucous-winged Gulls (*Larus glaucescens*) with respective densities of 10.4 and 5.6 birds km^{-2} (Kaiser et al. 1991, Campbell et al. 1990). Other fish-eating birds constituted less than 10% of summer observations.

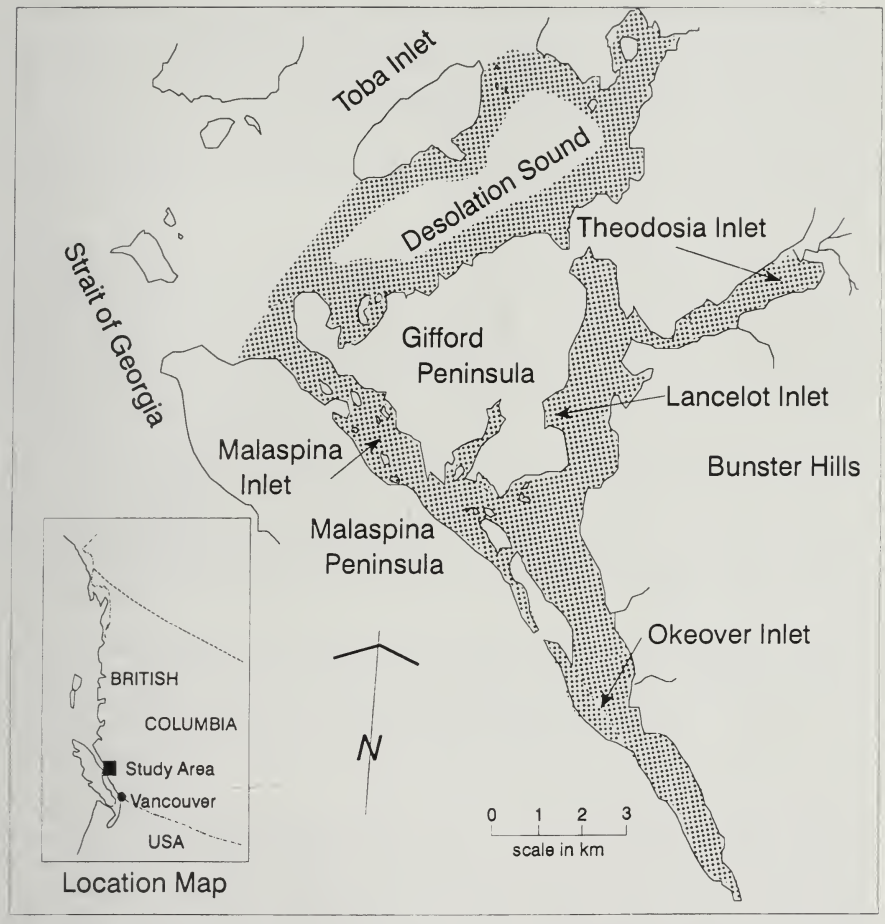

FIG. 1. Map of the Okeover Inlet study area on the eastern shore of the Strait of Georgia, British Columbia. Systematic surveys were made parallel to the shoreline to cover the entire shaded area. Additional observations of feeding flocks were made in the same area.

Between 6 June and 8 August 1991, we conducted 27 surveys along a 72.4 km transect route to determine the composition and density of mixed feeding flocks. We travelled at a continuous speed of 20 km h^{-1} and made observations out to 250 m on either side of the boat for an effective transect width of 500 m. Observations of flock duration and chronology, species' roles and interactions, and feeding methods were made independently of the surveys while stationary on the water about 50 m away from feeding flocks. Prey were identified visually with binoculars when they were driven to the surface by murrelets and when they were captured by gulls.

Results.—We observed 126 feeding flocks in whole or in part. The frequency of feeding flocks seen per survey was positively correlated to the total number of Marbled Murrelets observed per survey (Pearson correlation, $r = 0.66$, $N = 23$, $P < 0.01$). In 100 of the feeding

flocks Marbled Murrelets and Glaucous-winged Gulls were the only participants. Bonaparte's Gulls (*L. philadelphia*) were also present in 18 flocks, Common Mergansers (*Mergus merganser*) and Pigeon Guillemots (*Cepphus columba*) were each in three flocks, and Mew Gulls (*L. canus*) and Pelagic Cormorants (*Phalacrocorax pelagicus*) were each in one flock. California Gulls (*L. californicus*), Common Loons (*Gavia immer*), Pacific Loons (*T. pacifica*), and Surf Scoters (*Melanitta perspicillata*) occasionally were seen but did not participate in mixed-species feeding flocks. The proportion of murrelets seen per survey feeding in mixed species feeding flocks ranged between 1 and 22%, and was not correlated with murrelet density ($r = 0.19$, $N = 23$, $P > 0.05$).

The initiation of 27 mixed-species feeding flocks was observed. In every case, Marbled Murrelets feeding singly or in small groups (<5) initiated the flocks by driving a school of sand lances (*Ammodytes hexapterus*) to the surface where they thrashed briefly in a tightly packed "boil." This attracted one or two Glaucous-winged Gulls to the site, and if the sand lances kept resurfacing more gulls quickly arrived. Additional murrelets were also attracted but generally arrived more slowly than most of the gulls. Arriving singly or in groups of less than five, these murrelets usually swam, or less commonly flew, to the edge of the feeding area and began diving. Generally, murrelets were distributed loosely at the flock periphery, while gulls concentrated in a tight group in the center. Diving by murrelets appeared to keep the school of fish near the surface and accessible to gulls. Marbled Murrelets foraged by pursuit-diving while Glaucous-winged Gulls fed by dipping, surface seizing and surface plunging (Ashmole 1971). Throughout the duration of the feeding flock, both gulls and murrelets called frequently. No other diving birds were observed causing boils of fish, however similar boils by harbor seals (*Phoca vitulina*) did attract gulls but did not result in feeding flock formation.

First-year sand lances (6–10 cm) were the only prey identified in feeding flocks. Three SCUBA dives made in the vicinity of feeding flocks confirmed the presence of schools of sand lances within 5 m of the surface. In the evenings, we saw murrelets holding larger sand lance (14–18 cm), Pacific herring (*Clupea harengus*), and shiner perch (*Cymatogaster aggregata*), which likely were destined for nestlings (Carter and Sealy 1987), but none of these species was taken during mixed-species feeding events.

Feeding flocks were generally small, with a mean of 7.7 murrelets (range 1–48) and 5.9 Glaucous-winged Gulls (range 1–33, $N = 126$). The largest feeding flock consisted of 48 murrelets and 14 gulls. There was a significant positive correlation between the numbers of murrelets and gulls in each mixed-species flock (Fig. 2). The relationship was non-linear and the best fit was obtained with a logarithmic curve indicating that gull numbers approached an asymptote despite increasing numbers of murrelets (Fig. 2, $r = 0.76$, $N = 46$, $P < 0.005$). The ratio of gulls to murrelets in flocks with up to 16 murrelets was approximately one to one but declined with increasing flock size.

Mixed-species feeding flocks lasted 1–79 minutes. Flock duration was positively correlated with the number of participating murrelets ($r = 0.94$, $N = 41$, $P < 0.005$). Feeding ended abruptly. Most murrelets simultaneously ceased to dive and slowly drifted away from the feeding area. Gulls also dispersed on the water as the murrelet's diving activity ceased, and they flew away after 1–2 min if no new boils of fish appeared.

Discussion.—Our observations of murrelets contrast sharply with low flocking tendencies (0.2%, Porter and Sealy 1981) and infrequent feeding flock initiation (1.4%, Porter and Sealy 1982; 15.9%, Chilton and Sealy 1987) seen on the west coast of Vancouver Island. Similarly, in Washington and Alaska, Marbled Murrelets participated in only 2% and 0.6%, respectively, of mixed-species feeding flocks and were never seen to initiate such flocks (Hoffman et al. 1981). In the Okeover Inlet Area in 1990, however, the murrelets frequently participated in mixed-species feeding flocks and initiated all of the flocks we saw from the start.

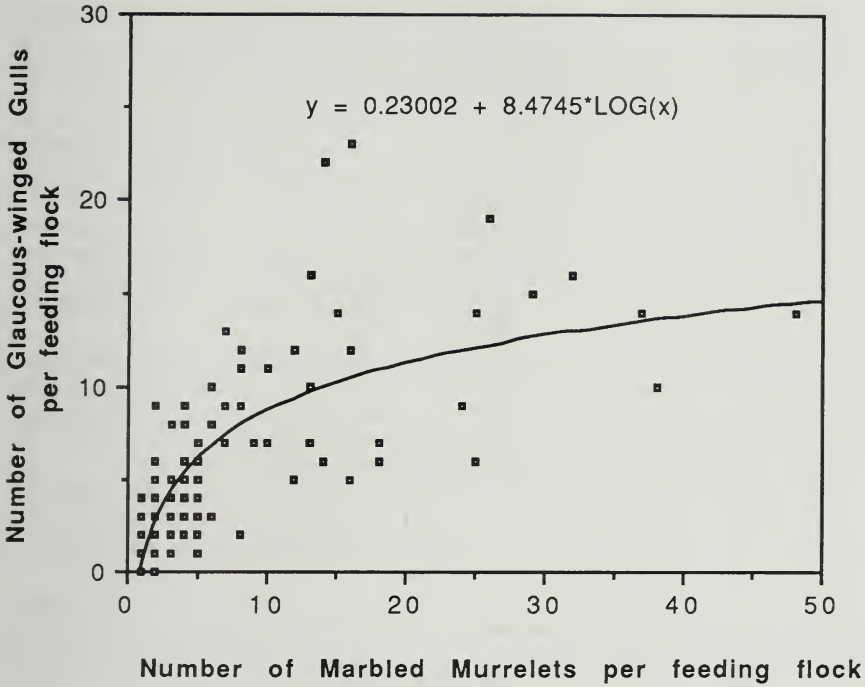

FIG. 2. Numbers of Marbled Murrelets and Glaucous-winged Gulls recorded in feeding flocks. The equation and line show the best-fit logarithmic relationship.

Several factors may have encouraged greater flocking behavior by murrelets in the study area. First, larger more aggressive alcids, such as Common Murres (*Uria aalge*) which can disrupt feeding in smaller alcids (Chilton and Sealy 1987, Piatt 1990), were absent. Second, the study area contained very high densities of murrelets (10.4 birds km^{-2}, Kaiser et al. 1991) which may be important because we found a positive correlation between murrelet density and the number of feeding flocks. Third, prey were locally concentrated and their behavior of balling up at the surface when attacked likely facilitated flock formation (Grover and Olla 1983). It seems unlikely that the prey type itself could explain the flocking behavior, since sand lances are common prey for murrelets in Barkley Sound where murrelets rarely join mixed-species flocks (Carter and Sealy 1990).

The aggregation of murrelets over schools of sand lances may be an example of intraspecific cooperative foraging. Fish schools may be more vulnerable when attacked by several birds (Gotmark et al. 1986). We found that flock persistence was positively correlated to the number of murrelets in the flock. The "boiling" of dense schools of fish at the surface is believed to confuse underwater predators and reduce the surface area of the school available for exploitation (Grover and Olla 1983, Girsa and Danilov 1976). However, alcids have been seen herding sand lances (Angell and Balcomb 1982) and may be able to control surface concentrations by preventing their escape, thus increasing the period during which the fish can be exploited (Hoffman et al. 1981, Grover and Olla 1983).

The frequent association of Glaucous-winged Gulls with individuals and pairs of diving

murrelets and the gulls' immediate response to "boils" of sand lance suggests that some gulls have learned to monitor the murrelets. Once a flock is initiated, the conspicuous white plumage and active feeding method of gulls serves as a catalyst for the attraction of other flock participants (Armstrong 1971, Gotmark et al. 1986).

Flocks with up to 16 murrelets usually had equal numbers of gulls and murrelets. As the number of murrelets increased, the number of gulls remained approximately stable although new individuals arrived and displaced gulls already feeding. This dynamic equilibrium appeared to be established through interference competition among the gulls for a limited area on the water where they could successfully exploit the ball of sand lance. The number of murrelets did not show a similar plateau probably because they foraged in three dimensions with a larger exposure to the ball of fish (Baltz and Morejohn 1977). In addition, physiological limitations of diving reduced the total time murrelets could exploit the school underwater. For 126 dives the dive : pause ratio was 2:1.

Initiators are species which locate prey concentrations and typically include surface feeders such as Glaucous-winged Gulls (57%, Chilton and Sealy 1987) or Black-legged Kittiwakes (*Rissa tridactyla*) (76%, Hoffman et al. 1981). Although Glaucous-winged Gulls were numerous and schools of sand lances were observed near the surface, Marbled Murrelets started all of the mixed-species feeding events we observed in the Okeover Inlet area.

This study demonstrates that Marbled Murrelets can regularly feed in flocks under favorable conditions where interference from larger diving birds is lacking. Our study also emphasizes the important, often underestimated role that diving birds play in initiating and maintaining mixed-species feeding flocks of seabirds.

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TODD E. MAHON, *Dept. of Biology, Univ. of Victoria, P.O. Box 1700, Victoria, British Columbia, Canada V8W 2Y2;* GARY W. KAISER, *Canadian Wildlife Service, P.O. Box 340, Delta, British Columbia, Canada V4K 3Y3;* AND ALAN E. BURGER, *Dept. of Biology, Univ. of Victoria, P.O. Box 1700, Victoria, British Columbia, Canada V8W 2Y2.* *Received 23 July 1991, accepted 1 April 1992.*

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Arthropod feeding by two Dominican hummingbird species.—Hummingbirds are predominantly floral nectar feeders (Montgomerie and Redsell 1980) and are thought to be closely tied to flowers through most or all of their life cycle (Wolf 1970). Although hummingbirds forage extensively on insects and other arthropods (Wagner 1946; Stiles and Wolf 1970, 1979; Feinsinger and Colwell 1978; Montgomerie and Redsell 1980), arthropods as food are not well known in comparison with nectar (Remsen et al. 1986). Because nectar is high in calories and because hummingbirds have great energy requirements, detailed studies of hummingbirds have assumed that energy is the most important variable determining their behavior. Arthropods may not be a crucial or limiting resource for hummingbirds (Feinsinger 1976, Wolf et al. 1976, Feinsinger and Colwell 1978) and may represent only a limited energetic component of diets (Wolf and Hainsworth 1971). Hainsworth (1977), however, suggests that an equal time flycatching by hummingbirds, even with low efficiency rates of 40%, can provide more energy than nectar feeding.

Detailed foraging studies (reviewed in Gass and Montgomerie 1980) report foraging for insects by hummingbirds as generally less than 15% of feeding time (Wolf and Hainsworth 1971, 1977; Hainsworth 1977), however, other studies report searching for arthropods as the bulk of foraging effort (Young 1971) or, at times, the only food taken (Kuban and Neill 1980). Several studies of hummingbirds show that under field conditions some humming-

birds feed exclusively on arthropods for short periods of time (Wagner 1946, Kuban and Neill 1980, Montgomerie and Redsell 1980). A recent study (Remsen et al. 1986) shows an unexpectedly high frequency of arthropods in hummingbird diets from Bolivia, Peru, Costa Rica, Venezuela, and Panama. It was found that 79% (1279 of 1629) of examined hummingbird stomachs and crops contained arthropod remains. It appears that insect feeding by hummingbirds is not incidental or opportunistic but probably occurs regularly in many species (Remsen et al. 1986). Foraging for arthropods by hummingbirds may be in response to abundant insects or may be a necessary alternative during nectar shortages (Wagner 1946, Young 1971). Whatever the reason for arthropod foraging by hummingbirds it appears more widely spread than previously considered.

Here we report observations made on the insect feeding of the Purple-throated Carib (*Eulampis jugularis*) and Green-throated Carib (*E. holosericeus*) in the tropical dry forest of Dominica, West Indies. The diet of these species contained high percentages of arthropods captured by gleaning on leaves and flowers or by flycatching. The Purple-throated Carib is known to forage on insects (Wolf and Hainsworth 1971, Lack 1973) but in Dominica is reported spending less than 1% of total foraging time searching for insects. The Green-throated Carib's diet is not well documented but it probably also consumes insects (Lack 1973).

The Purple-throated and Green-throated caribs are distributed throughout the Lesser Antilles in the West Indies. The Green-throated Carib occurs in all islands of the Lesser Antilles and Puerto Rico (Bond 1985). It seems to prefer forest clearings and inhabits primarily lowland areas (Lack 1973, Bond 1985). The Purple-throated Carib occurs in all the mountainous islands of the Lesser Antilles except Grenada (Lack 1973). This species is found both in the forest (Lack 1973) and clearings (Bond 1985) from sea level to 1200 m (Wolf and Hainsworth 1971). In Dominica both species are common and were observed regularly throughout the island.

Methods.—We studied hummingbirds on the Archbold Tropical Research Center, Springfield Field Station, located on the western side of the island at an elevation of 380 m. The vegetation here is lowland rainforest (Bullock and Evans 1990) or deciduous forest (Nicolson 1991). The deciduous rainforest is considered a transitional community between the lower dry scrub woodland and the higher evergreen rainforest. The area studied contains patches of typical primary forest, secondary forest, and areas of cultivation (banana, coffee, and citrus) either in use or overgrown with vines and other secondary invaders. We observed foraging by hummingbirds at three different sites in the forest for periods of 1 to 2 h between 08:00 and 11:00 h EST or 12:00 and 17:00 h EST between 27 May and 14 June 1991. The three sites were undisturbed primary forest, a forest gap, and an old abandoned field. We observed hummingbird foraging activity for 31 h. At each feeding attempt observed, we recorded the food item (nectar or arthropod) taken by each individual and the substrate from which it was taken (19 h of observation). The other 12 h of observation were divided into three, 2-h observation periods conducted on each of two territorial Purple-throated Caribs to determine time activity budget in relation to foraging. The two territorial caribs were in two contrasting sites. One territory was in a landscaped garden composed mainly of torch plants (*Alpinia purpurata*), with scattered heliconias (*Heliconia* spp.) located near the entrance to the station headquarters. The second territory was located in primary forest, in a ravine with the ground strata dominated by heliconia plants with a few scattered torch plants.

All sites where caribs were observed foraging had flowers of one or more species present, although the number of flowering plants was low. The species observed flowering during the study period include *Heliconia caribea, Psittacanthus martinicensis, Inga ingoides, Passiflora* spp., *Lantana* spp., and *Musa* spp. Despite the many flowering species present, during

the season in which our observations were made, few flowering plants, except heliconias, were observed in significant numbers throughout the forest.

Results.—During the 19 h of observations, 18 Purple-throated Caribs and 13 Green-throated Caribs were observed feeding. The majority (94.4%, N = 42) of Purple-throated Carib feeding attempts were directed at arthropod prey. Most arthropod prey items (61%) were gleaned from plant substrates, such as flowers, leaves, and branches and also by flycatching (33.3%). Most insects (63.1%) taken from substrates were gleaned from *Heliconia* inflorescences. A difference between nectar and insect feeding was readily apparent when observing caribs feeding on flowers. When taking insects from flowers the caribs gleaned (Remsen and Robinson 1990) rapidly from the outside of the flower corolla, while when taking nectar the birds probed (Remsen and Robinson 1990) between the petals. Green-throated Caribs were observed feeding on arthropods 100% (N = 31) of the time. Most prey (92.3%) was taken from the air by flycatching or sally-hovering while 7.6% of observations were of Green-throated Caribs gleaning insects from branches.

The time spent foraging by the two territorial Purple-throated Caribs was similar. The carib in the torch plant site spent 21% of time foraging while the carib in the forest territory spent 23% of time foraging. Foraging for insects differed greatly between the two caribs. At the torch plant site the carib spent 20% of foraging time feeding on insects and 80% of time feeding on nectar. By contrast, in the forest territory the carib spent 92% of time feeding on arthropods and only 8% feeding on nectar.

Discussion.—All female Caribs and Antillean Crested Hummingbirds (*Orthorhyncus cristatus*) captured during other phases of field work during the study period possessed a brood patch. The presence of the brood patch in examined birds, in addition to four nests that we found (2 Purple-throated Carib, 2 Antillean Crested Hummingbird) in early stages of construction (2 nests) or with eggs (2 nests), suggest our observations occurred during the reproductive period of these species. The high protein costs associated with egg production in birds may stress a female's daily energy balance (Ricklefs 1976, Walsberg 1983). Whether arthropods are used as a source of proteins by female hummingbirds during the reproductive period is not known. Some frugivorous and granivorous passerine birds make use of insects during parts of the breeding season, particularly to feed young during the early stages of nestling development (Morton 1978). In frugivorous birds, insects are considered to be more important than fruit availability in determining breeding cycles of birds in Costa Rica (Levey 1988). Concerning hummingbirds Montgomerie and Redsell (1980) made observations of a nesting female and report that it fed exclusively on arthropods over a two week period. Information regarding hummingbird use or importance of arthropods previous to egg laying or during the rearing of young is needed.

The high percentage of arthropod food items taken by the caribs studied here may be a response to a low availability of nectar due to decreased density of flowers during the dry season. During this season insects may serve as an alternate food resource. A second alternative is that the caribs are not undergoing a shortage of floral nectar but are making use of arthropods because they are present in abundance throughout the habitat and are easily captured. Remsen et al. (1986) have proposed that most hummingbirds feed on arthropods routinely, perhaps on a daily basis, and probably at regular intervals throughout the day. Our observations tend to support this idea, since all studied caribs were observed consuming arthropods. Even the Purple-throated Carib in the torch plant territory, in which nectar producing flowers were present in great numbers, spent 20% of foraging time feeding on arthropods.

Hummingbirds in areas with distinct wet and dry seasons, as in Dominica, may utilize distinct foraging strategies during the different seasons. Wagner (1946) found that, in areas of Mexico with a pronounced dry season, hummingbirds live chiefly on insects. Wolf (1970)

discovered that in Costa Rica during the early part of the dry season hummingbirds take mostly insects while taking large amounts of nectar during portions of the rainy season. Because of the hummingbird's small size and limited capacity to store energy, it is of vital importance that it adjust rapidly to changing food resources (Stiles and Wolf 1970). It is necessary to study the foraging behavior of the Dominican caribs during both the wet and dry season to determine if they are simply adjusting to changing food resources, using arthropods only seasonally during the breeding period, or if they feed regularly on arthropods throughout the year.

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FELIPE CHAVEZ-RAMIREZ AND MCALISTER DOWD, *Dept. of Wildlife and Fisheries Sciences, Texas A & M Univ., College Station, Texas 77843.* *Received 28 Jan. 1992, accepted 15 April 1992.*

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Behavior of polygynous and monogamous Loggerhead Shrikes and a comparison with Northern Shrikes.—Reports of polygyny in *Laniinae* are rare (Verner and Wilson 1969). To date, polygyny has been recorded only once in Loggerhead Shrikes (*Lanius ludovicianus*) (Verner and Wilson 1969) and in one study in Northern Shrikes (*L. excubitor*) (Yosef and Pinshow 1988). Additional records will allow us to understand prevailing conditions, strategies adopted, and the costs and benefits of being polygynous.

Methods.—Two polygynous and 23 monogamous Loggerhead Shrikes were studied at the MacArthur Agro-ecology Research Center, Archbold Biological Station, Lake Placid, Florida. This 4120-ha cattle ranch consists primarily of improved pasture, with scattered cabbage palm (*Sabal palmetto*) hammocks, native wetlands, and live oak (*Quercus virginianus*) uplands.

Time-budgets were constructed for all pairs included in the study. The birds' diurnal behavior was divided into (1) perching, (2) flying (to or from collecting prey, chasing conspecifics or heterospecifics, or changing lookout points), (3) handling prey (recorded from the instant the shrike landed on or near the prey and attacked it until the prey had been impaled or consumed), and (4) preening.

Males were captured with either a bal-chatri noose trap or treadle trap and color banded. Territories were mapped by plotting points of shrike activity and by observing their reaction to taped songs of other males, and to a mounted specimen. Data are presented as mean ± SD.

Results and discussion.—Monogamous males captured 7.2 prey per hour as compared to 9.3 in polygynous males. Monogamous males captured mainly insects, the rest being reptiles. Although polygynous males also captured mostly insects, they also caught amphibians and reptiles. Territories of polygynous males did not differ in area from those of 23 monogamous males ($U_{2,23} = 39$, $P < 0.1$), although the total number of nestings attempted per territory

Table 1

Prey Capture Rates, Dietary Composition, and Reproductive Success of Monogamous and Polygynous Northern and Loggerhead Shrikes

	Northern Shrike		Loggerhead Shrike	
N	Monogamous 5	Polygynous 2	Monogamous 23	Polygynous 2
Prey/h	0.59	1.19	7.2	9.3
Arthropods	95.4	89.4	97.3	86.3
Amphibians	—	—	—	6.7
Reptiles	4.6	7.4	2.7	7.0
Birds	—	2.7	—	—
Mammals	—	0.4	—	—
Number of nesting attempts	1.8 ± 0.5[a]	3.5 ± 0.7[b]	1.7 ± 0.6[a]	4.0 ± 0.0[b]
Total number of eggs laid	9.4 ± 2.5[c]	18.5 ± 3.5[d]	9.2 ± 2.7[c]	18.5 ± 2.1[d]
Total number of young fledged	—	—	7.0 ± 2.5	13.5 ± 2.1

Records with the same superscript are not statistically significantly different ($P > 0.05$). Capture rates and measures of reproductive success are given as mean ± SD.

($U_{2,23} = 46$, $P < 0.005$), eggs laid per territory ($U_{2,23} = 46$, $P < 0.005$), and young fledged per territory ($U_{2,23} = 45$, $P < 0.01$) were significantly larger.

Two polygynous Loggerhead Shrike males fed their young 477 times (4.3 ± 2.8 per h), while monogamous males 372 times (5.1 ± 2.3 per h). Females of polygynous males adopted different nesting strategies than females of monogamous males. I termed these 'parallel' and 'serial' strategies. In the 'parallel' strategy, females of polygynous males laid a second clutch within 10 to 12 days after the first hatched, and only the males continued to care for the first brood. Also, in this strategy females tended nests that were 'spaced out in time'. "Spaced out in time" means a situation in which the second female laid eggs only after the nestlings of the first female had hatched. The polygynous male worked at a constant rate, feeding the two females and their young. In the 'serial' strategy, females of monogamous males laid the second clutch only after the first brood fledged. In both strategies, males provided parental care up to several weeks after the young fledged.

Comparisons between contemporaneous observation periods of fixed length revealed that polygynous male Northern Shrikes spent significantly more time than monogamous males seeking and handling prey (Yosef et al. 1991). Males usually brought food to the vicinity of the nest and passed it to the female or impaled it at cache sites, and females retrieved cached food themselves. However, polygynous Loggerhead Shrike males, like their monogamous counterparts, fed and tended young. Females of both species, in monogamous and polygynous relations, relied on males to supply most, if not all, of their food requirements during the pre-nesting, incubation, and pre-fledging periods.

Assuming that apparent reproductive success equalled realized reproductive success for Northern Shrikes, polygynous males fathered nearly twice as many eggs as monogamous males. This assumption is corroborated by the data for Loggerhead Shrikes wherein polygynous males fledged almost double the number of young than monogamous males. However, the increased egg production in Northern Shrikes, and fledging of young in Loggerhead Shrikes, was not without cost: polygynous males hunted more on exposed sites and may have been exposed to greater predation risks and energetic costs.

Adaption of the 'parallel' reproductive strategy may allow males to conserve energy and maintain nutritional condition. Degen et al. (1992) demonstrated that male Northern Shrikes were able to maintain the lowest reported energy costs for adult birds feeding altricial young, and Yosef and Pinshow (1989) showed that males create large caches prior to the breeding season. The cached prey augment the fresh prey and help reduce energetic costs. In this manner, males are never in a situation wherein they feed more than one brood at a time. Although the total investment of males during various nesting stages remains unknown, this result is of importance because Loggerhead Shrikes are also capable of changing strategies, but the energetic consequences remain to be studied.

Loggerhead Shrikes display flexibility in their capability to live off the more abundant prey species during different seasons of the year. They may also enhance their fitness by choosing between alternate reproductive strategies dependent on the abundance of food resources in caches and in the territory.

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Reuven Yosef, *Dept. of Zoology, 1735 Neil Avenue, The Ohio State Univ., Columbus, Ohio 43210; and Archbold Biological Station, P.O. Box 2057, Lake Placid, Florida 33852.* *Received 30 Jan. 1992, accepted 18 April 1992.*

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The waving display and other nest site anti-predator behavior of the Black-capped Chickadee.—Adult Black-capped Chickadees (*Parus atricapillus*) and other *Parus* spp. show conspicuous postures and movements directed toward potential predators at the nest site (Odum 1941, Dixon 1949, Hinde 1952, Laskey 1957, Betts 1958, McLaren 1976, Long 1982). Descriptions of these displays, called "injury-feigning" (Pettingill 1937, Odum 1941, McLaren 1976) and "distraction" (Hinde 1952, Laskey 1957, Long 1982, Smith 1991) displays, often are incomplete and have not been defined consistently in the literature. Some descriptions are inconsistent among different authors (Long 1982), suggesting that the display is either highly variable or that more than one display is involved. Furthermore, the name "distraction" for the display implies a function for which there is currently no evidence and for

which alternative functions exist. This paper re-examines anti-predator behavior using video recordings and slow-motion analysis with the objective of redescribing the behavioral components in greater detail. We suggest the name "waving" for this primarily visual display to depict the noticeably slow movements of the body and wings. In addition, we presented study skins of potential predators to chickadees at the nest site to determine which predators elicit specific behaviors.

Methods.—Observations were made in June 1990 at Picnic Point on the campus of the Univ. of Wisconsin–Madison. Four adult Black-capped Chickadees, two mated pairs, were observed displaying near their nests in holes excavated about 1 m above ground in rotting snags. The nestlings were 7–10 days of age. Study skins of an eastern chipmunk (*Tamias striatus*), gray squirrel (*Sciurus carolinensis*), Blue Jay (*Cyanocitta cristata*), Eastern Screech-Owl (*Otus asio*), and a House Wren (*Troglodytes aedon*), were presented to two other mated pairs of chickadees during five days from 5–13 June 1991 when the nestlings were 8–16 days of age. Both pairs were nesting in boxes about 1 m above ground at Picnic Point and the nearby residential area of Shorewood Hills. Each predator was presented one at a time in varied order at two distances from the nestboxes; on the ground 1–3 m from the nestbox and on a branch $\leq$½ m or on top of the nestbox. One pair was tested on three days, and the other pair was tested on four days with one to three different predators being presented on a given day. The observers stood 5–10 m from the nest to record the reactions of the birds. Individuals could be identified by unique color-band combinations. The birds' reactions were recorded with a VHS RCA CC520 Pro Edit Video Camcorder (scanning specifications = 525 lines/60 fields/30 frames per sec). Recordings were made on a Polaroid Supercolor Plus 246 m video cassette tape with the camcorder set on super long play. Some of the trials were recorded with a Sony Handycam CCD-F77. The recordings were viewed on a Sony Multichannel TV Sound KV-2084R. Screen pictures on the TV were captured with freeze-frame control and sketches of the birds' postures were traced from these.

Results.—Different predators elicited different behavioral combinations. Using terminology of previous authors whenever appropriate (see Hinde 1952, Stokes 1962a, Smith 1972), these are as follows. (1) Head forward. The head is lowered to align with the longitudinal axis of the body and the neck is extended anteriorly. The bill is pointed in the direction of the predator. When the predator is below the bird, the bird may tip down anteriorly, such that its head is lower than its tail. (2) Wings raised. The wings are rotated outward so that the leading edge of the wing is lifted away from the body. The wing tips may separate from the tail to a varying degree, but usually not more than 45° laterally from the longitudinal axis. The wing tips are sometimes held below the level of the tail and sometimes above. (3) Body wave (Fig. 1C). The bill and neck are extended in the head forward posture (above) and the head is moved slowly from side to side at a rate of about 1 cycle every 5 sec, or 0.2 cycles/sec, for a variable length of time. The side to side movement usually includes the body as it aligns with the head, and sometimes the tail. The slow movement and stiffened appearance of the neck and head during body waving contrasts with the scanning head movements of a bird in a relaxed perch position. The side-to-side movement may also resemble the motion of a pendulum, with the head held high at either end of the arc and dipping down and then back up again during the course of the swing. (4) Wing wave (Fig. 1A, B). One or both wings are elevated above the longitudinal axis so that the inner linings are exposed to view. The raised wing is rotated forward, down, and back up in a rowing motion at a rate ranging from 1–5 cycles/sec ($\bar{x}$ = 3 cycles/sec). Higher intensity wing waving where the wings are more fully extended occurs at slower rates than less intense waving. The circular motion of the wings is repeated a variable number of times. This movement results in the flashing of the white inner linings of the wing. (5) Waving display. Behavior involving wing waving or body waving or both. (6) Body flick. In one

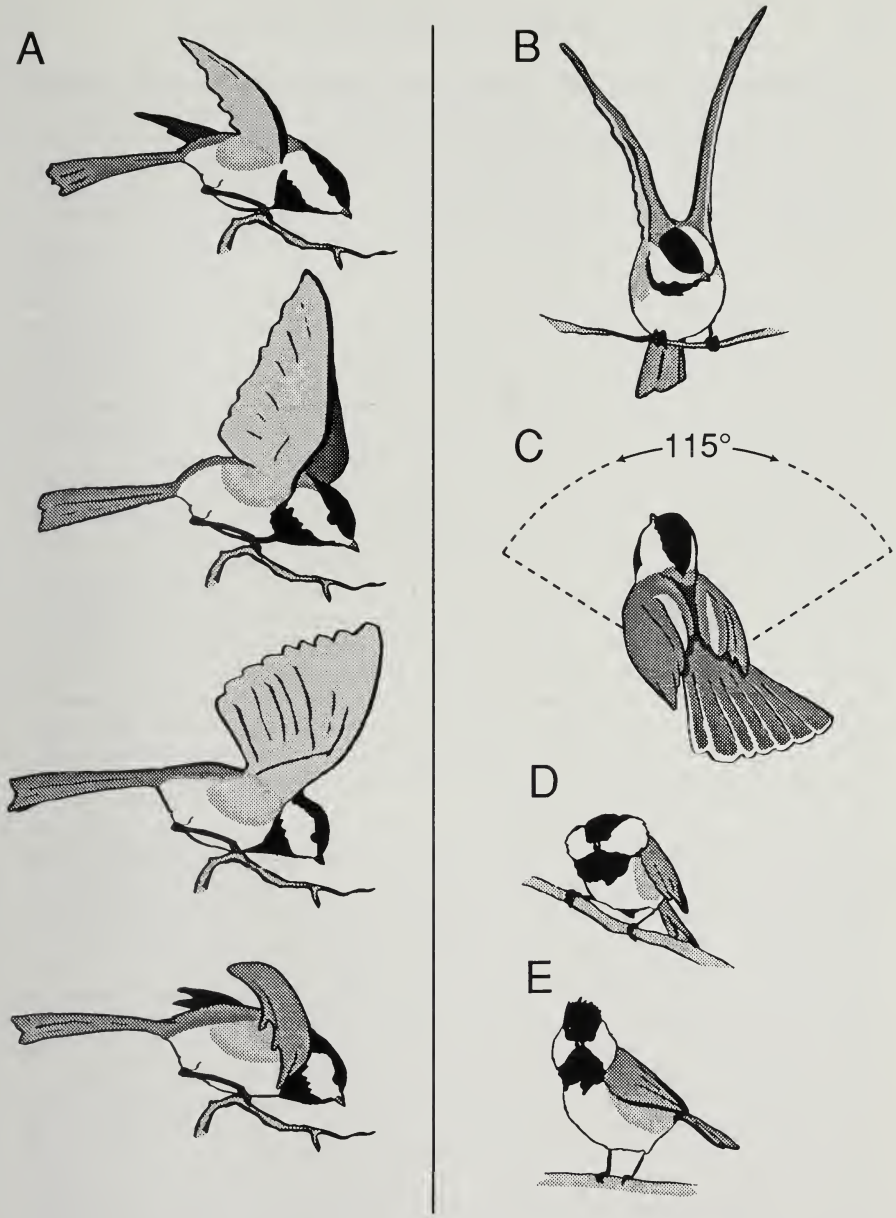

FIG. 1. Some behavior patterns that occur in the waving display (traced from video recordings displayed on a screen). A. Sequence of movements showing wing waving. B. Anterior view of the upward extension of the wings during wing waving. C. Body waving, showing the angle of side to side movement. D. Wide face, produced by raising feathers on the cheeks and sides of the neck combined with depression of feathers on the crown. E. Long face, produced by raising feathers on the crown, combined with normal or depressed feathers on the cheeks.

case while a bird was perched above a stuffed wren, it thrust its body vertically downward with its bill pointing at the wren, then raised its body back to normal perch position in a single motion lasting about 0.3 sec. The act was repeated two more times over the course of a min. (7) Feather postures. Various degrees and patterns of feather erection or depression give further expression to the above behavior patterns. In some cases the feathers on the cheek (cheek ruffle), sides of the neck, and nape (nape crest) were raised and the feathers on the crown were flat (crown sleek), giving a wide appearance to the face (Fig. 1D). The wide face sharply contrasted with the long face, which was produced by raised feathers on the crown (crown ruffle) and flattened or normal feathers on the cheek (Fig. 1E). Both long and wide faces were observed during head forward, wing wave, and body wave. In one waving display, a male had feathers erected throughout the torso (body ruffle) and on the crown. (8) Wing flick. The wing is quickly raised and brought back to rest in a single motion of about 0.07 sec in duration. (9) Tail flick. The tail is either quickly moved up and down or vibrated for about 0.07 sec such that the tail appears as a blur during slow motion playbacks. (10) Wing quiver. The tips of the wings are extended laterally and retracted again in a rapid motion of about 15 cycles/sec. The movement is repeated continuously for a variable amount of time, ranging from only a few cycles to several min of quivering. Wing quivering was frequently observed during bouts of antipredator display behavior, but it may not have been a reaction to the predator (see below). (11) Dive. The bird flies directly at the predator but does not make contact with it. (12) Attack. The bird flies directly at the predator and makes contact with it. (13) Open beak. The beak is held open. (14) Miscellaneous. Other forms of behavior given in the presence of potential predators included spreading of the feathers in the tail (tail fan) and extension of the legs. During wing waving, the bird frequently moved along the branch or to lower perches with a slow hopping motion that nearly resembled walking (only one foot left the perch at a time, but at some point both feet were off the perch). The birds were usually quiet during wing and body waves, but produced "hisses" on two occasions while lunging forward in the direction of the predator. Hissing occurred more frequently during dives and attacks.

Reactions to the study skins that occurred at least once are given in Table 1 for the different predator contexts. Some acts were more specific, occurring in the presence of some predators but not others. For example, wing waves and body waves occurred only during the presentations of the chipmunk and squirrel, whereas other acts, such as crown sleeks and nape crests occurred in all contexts. The combination of acts was highly variable, but a few generalizations follow. Tail fans occurred with wing waves, body waves, and attacks; hissing occurred with wing waves, dives, and attacks; crown ruffles occurred during wing waves, body waves, and with chick-a-dee calls; and wing and tail flicks occurred during bouts of chick-a-dee calling and sometimes preceded attacks and dives.

Two components, wing quivering and open beak, were probably not reactions to predators. Wing quivering occurred in all contexts, but in five of the six cases, the female wing quivered just as either she or her mate or both birds arrived together at the nest site or emerged from the box. In the sixth case where the female wing quivered, the position of her mate was not recorded. Around the nest site, wing quivering is given in the presence of the mate and is used to coordinate nestling care (Lambrechts et al., in press). Open beak was given by a female when her mate, who was in the head forward posture, was perched less than 0.5 m from her. While the female's beak was open, her head was turned away from the predator and toward her mate. The male then also opened his beak.

Although different predator contexts shared display components, the frequency of occurrence of these components varied widely (Fig. 2). Chick-a-dee calls occurred in most contexts, but, whereas it was the only one of five acts given in the presence of the jay or owl, it was

TABLE 1
DISPLAY COMPONENTS GIVEN TO DIFFERENT PREDATOR MODELS

Components	Eastern chipmunk	Gray squirrel	House Wren	Blue Jay	Screech-Owl
Wing wave	X	X			
Body wave	X	X			
Head forward			X		
Crown ruffle	X	X		X	X
Crown sleek	X	X	X	X	X
Nape crest	X	X	X	X	X
Cheek ruffle	X		X		
Cheek sleek	X	X			
Tail fan	X	X			
Dive	X	X	X		
Attack	X	X	X		
Hiss	X	X			
Chick-a-dee call	X	X	X	X	X
Wing flick	X	X		X	
Tail flick				X	
Body flick			X		
Hop	X	X			
Leg extension	X				
Wing quiver[a]	X		X	X	X
Open beak[a]		X			

[a] Probably not reactions to predators (see text).

rarely given in the presence of the chipmunk or squirrel. Dives and attacks occurred only with the chipmunk, squirrel, and wren predators, and the waving display occurred only with the chipmunk and squirrel predators. Although the experimental sample sizes were smaller, the results were similar when the predator was presented at greater than 1 m distance from the nest, with the exception that dives, attacks, and hisses dropped out. The frequency with which the other displays were given, however, tended to decrease with the greater distance.

The reaction to the owl and jay, i.e., chick-a-dee calling, wing and tail flicking, and frequent perch changes, contrasted so sharply with the reaction given to the chipmunk, i.e., the quiet waving display and/or hissing and attacks, that we decided to further test the differences in responses by switching the chipmunk model with the owl or jay, and vice versa, in front of the chickadees. Although these tests were performed only three times, the changes in responses occurred completely and immediately within a few seconds of the switch. Hence, the qualitative differences in reactions given to the different predators held true whether we presented the predators on different days or one consecutively after the other.

In addition, in 1990 chickadees were observed displaying to live chipmunks on ten occasions, both alone and near their mates. In eight of the ten occasions the displayers were oriented toward an eastern chipmunk on the ground within 2 m of the nesthole stump. Although chipmunks were not noted in the other two occasions, their presence may have been obscured by thick ground cover. The chipmunks gave no apparent reaction to the birds' displays, but merely passed by the nesthole stumps while foraging. The displays

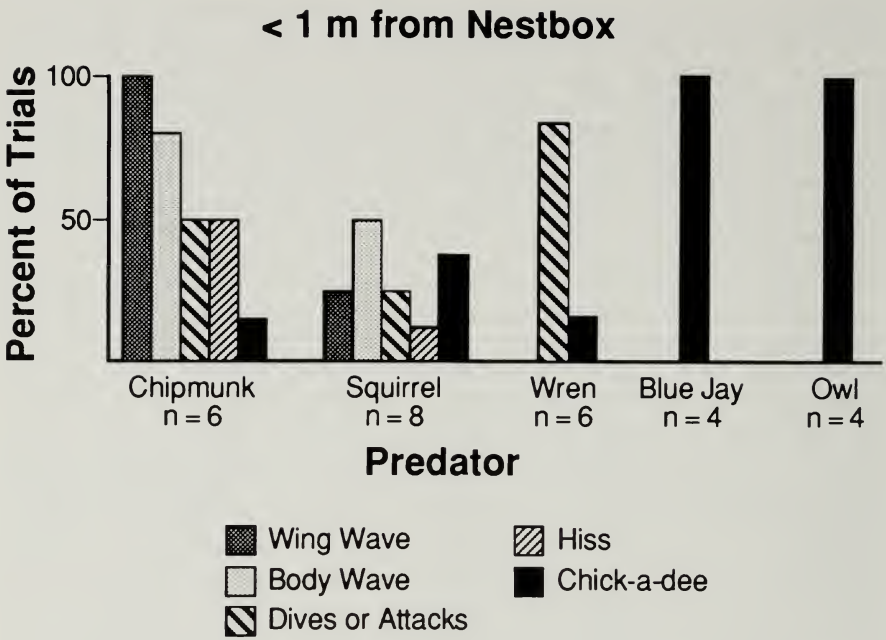

FIG. 2. The frequency of occurrence of five behavior patterns of chickadees when different types of predators were presented at a distance of less than 1 m or in contact with the nestbox.

included any number and variety of postures and movements, including wing waves, body waves, tail fans, crown sleeks, nape crests, leg extensions, hopping along the perch toward the chipmunk, and hisses.

In 1991 we made six observations of reactions to live Blue Jays, one to a live cat (*Felis domestica*), and one to a live raccoon (*Procyon lotor*) within 20 m of the nest. In each case the chickadees responded with chick-a-dee calls. On several occasions one bird assumed the head forward posture and dived at a human opening the nest box.

Discussion.—We used the same names for behavior patterns described in other studies for Black-capped Chickadees or other *Parus* spp. whenever it appeared that the behavior in each species was the same or homologous. For example, chickadees frequently raised their wings during the body wave in a manner that resembled the wings raised act described and photographed during agonistic encounters of the Great Tit (*P. major*; Hinde 1952, Fisher and Hinde 1949). Although Hinde (1952) stated that the wings may be raised above the level of the back, there was no mention of wing movement in the wings raised act as observed in this study. Hence, it seems appropriate to distinguish between wings raised and wing waving. In some cases, more than one name has been used to describe the same display. For example, "open beak" (Stokes 1962a) has also been called "gape" (Smith 1972, Smith 1991). We chose to go with "open beak" to distinguish it from the gaping action given by nestlings, fledglings, and sometimes females, which involves a wider opening of the mouth while calling for or receiving food.

The purpose or usefulness of the waving display at the nest site is not entirely clear. Previous observers described the display or similar components of the display as being either injury-feigning, distraction, or threat displays. Odum (1941) described an "injury-feigning"

display by a Black-capped Chickadee pair directed toward himself after capturing one of the newly fledged young. In both parents the wings were outstretched and slowly flapped over the back, and the head was held straight out and moved side to side. The display appeared to be elicited only by the cry of the young or when the cry of the young was imitated. Although the waving display we observed shares components with the "injury-feigning" display described by Odum (1941), our birds did not appear to be injured and there was no attempt to lead the predator away from the nest hole. In all of the 1990 observations where distance was noted, the chipmunks were 1–2 m from the nest, and the nesthole was frequently between the chipmunk and the bird that displayed. The birds usually remained stationary or shifted short distances along the perch or to nearby perches. Nevertheless, the slow waving motion may serve to attract and focus the attention of the predator on the displayer, thereby decreasing the chance that the predator will find the nest. Alternatively, the waving display may represent intention movements to convey aggressive tendencies or movements to make the bird appear larger or more menacing. At least some of the same components of the waving display are used in agonistic situations. In both Great and Blue tits (*P. caeruleus*), wings raised and head forward postures accompanied by raised feathers of the cheek and crown, open beak, body waving, and tail fanning occurred when a bird at the feeder was approached too closely by another bird (Hinde 1952). In Blue, Great, and Marsh tits, these behavior patterns correlated with the tendencies of birds to attack, escape, or stay (Stokes 1962a, b). Behavior resembling wings raised and head forward postures also occurs in agonistic interactions of the Carolina Chickadee (*P. carolinensis*; Brewer 1961) and Tufted Titmouse (*P. bicolor*; Wallace 1967). The threat display hypothesis may explain why the female we observed reacted to her mate by opening her beak when he displayed toward the predator model in the head forward posture near her. However, not all components of the waving display have been noted in agonistic interactions. Specifically, the waving motion of the wings has been described only in predator encounters.

Of particular importance are the different reactions chickadees have to different types of predators. In this study, only sciurids elicited wing waving, wrens and sciurids both evoked body waving and attacks or dives, and owls and Blue Jays elicited chick-a-dee calls. Long (1982) noted that a "distraction" display was given to study skins of various sciurids as well as to the House Wren and a live snake. However, Long did not distinguish between the various components of the display given in different predator contexts, thereby making comparisons with our results difficult.

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JANINE R. CLEMMONS AND MARCEL M. LAMBRECHTS, *Dept. of Zoology, Univ. of Wisconsin, Madison, Wisconsin 53706.* (Present address MML: *Centre National de Recherche Scientific, Centre d'ecologie functionelle et evolutive, Cepe L. Emberger, Route de Mende, BP 5051, 34033 Montpellier, Cedex, France.*) *Received 3 Dec. 1991, accepted 15 May 1992.*

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Peculiar behavior of a subadult female Tree Swallow.—I observed peculiar behaviors displayed by a dull-brown subadult (SY; Hussell 1983) female member of a trio of nesting Tree Swallows (*Tachycineta bicolor*) at the Creston Valley Wildlife Management Area, southeastern B.C. (49°05′N, 116°35′W), during May–June 1991. The range of behaviors exhibited by the SY female included typical parental breeding behavior, apparent "helping" behavior when the SY female tended only the offspring of the other female, and non-breeding (i.e., nest attendant) behavior when the SY female repeatedly took food from both the male and other female (cf Lombardo 1986, 1987a, b). The observations suggest that mistaken "helping" behavior may occur frequently in Tree Swallow trios (cf Quinney 1983) and that behavior in adult Tree Swallows during the breeding season has evolved considerable plasticity, perhaps in response to the unpredictable availability of nest-sites.

The trio of birds included an unbanded male, an after-second-year (ASY) female, and the SY female. The ASY and SY females were captured, banded, and painted on 30 May and 7 June, respectively, but the marked differences in plumage color enabled me to distinguish each bird prior to banding. The ASY female completed a clutch of five eggs on 23 May. The SY female was observed circling the box on 26 May while the ASY female was incubating, and she was also present when I banded the ASY female. On 2 June, I discovered eight eggs in the nest cup. Evidently, the SY female began laying on 31 May and she completed her clutch on 4 June when there were ten eggs in the nest cup. I marked the new eggs with a non-toxic permanent marker beginning 2 June. On 5 June one of the eggs of the ASY female began pipping, and by 7 June there were five nestlings belonging to the ASY female and five eggs belonging to the SY female.

Three 1-h watches were conducted (08:00–11:30 MST) at the nest on 7, 10, and 14 June, corresponding to nestling-days (ND) 2, 5, and 9. Watches were conducted from 45 m using 7 × 50 binoculars and a 15× spotting scope. After the first watch I captured the SY female while she lay on the ASY female, which was brooding the nestlings. The SY female was

found to have a large, non-vascular brood patch. When I recaptured her seven days later, she was lying on the nestlings, and her brood patch was vascular. It is likely that the SY female never directly incubated her eggs because they were covered by the ASY female's nestlings, particularly as the nestlings grew.

The parental and "helping" behavior exhibited by the SY female was considerable. She removed more fecal sacs (N = 6), defended the nest site from conspecific intruders more often (N = 5 chases), and spent more time on the territory (98/180 min = 54%) than either of the parents (fecal sacs, parents combined, N = 5; intruder chases, parents combined, N = 3; % time on territory, ASY female = 38%, male = 44%). She apparently brooded the young as indicated by her vascular brood patch, the fact that she was captured lying on the young, and her prolonged visits inside the box. The SY female spent 50% (30/60 min) of last watch inside the box compared to only 5% (3/60 min) by the ASY female. Evidence suggests that the SY female was feeding the young. I once saw the SY female enter with a large bolus of food. Also, the SY female entered the box (23 times in 180 min) at a rate comparable to that of the ASY female (24 in 180 min), and more often than the male (15 in 180 min). Lombardo (1987a) found that nearly 100% of parental visits to nests resulted in nestling feeding after ND 3. Finally, the SY female exhibited feeding behavior similar to that of the two parents.

All three adults were seen at the box until the young fledged on 27 June. The young were of comparable size and mass to other broods in the study area. After the young fledged, the eggs belonging to the SY female remained intact in the nest cup. They did not hatch, and they were not inspected for embryos.

During nest watches the SY female exhibited nest attendant behaviors on five occasions when she took whole or partial food boluses from the parents. In each instance the SY female was perched inside looking out of the hole where she met the incoming parent. This happened three times to the ASY female and twice to the male. Once the SY female took the bolus from the ASY female and swallowed it in plain view, but on the other four occasions she either went inside the box or flew off. The parents flew away on four of the five occasions, as if they had fed one of the young, and once the ASY female entered the box. Lombardo (1986, 1987a) found that attendants at Tree Swallow nests often beg for, or attempt to steal food from parents. Tolerance of such actions of nest attendants by parents may be due to the fact that attendants typically do not harm nestlings or significantly impede parents (cf Lombardo 1985, 1987b).

The "helping" behavior exhibited by the SY female arose due to reproductive error which likely resulted from the summation of various stimuli received from the nestlings, the feeding behavior exhibited by the parents and her motivation to care for young after completing her own clutch (Williams 1966). Examples of misplaced parental care have been reported in other species (e.g., Power 1975, Bollinger et al. 1986), and there are many accounts of interspecific feeding by birds (Skutch 1961, Shy 1982, Butler and Campbell 1987, Yoerg and O'Halloran 1991). Power (1975) noted that misplaced parental care is an inevitable result of strong selection on birds to care for their own young, so the behavior of the SY female is not surprising given the unique sequence of events that occurred in the nest. It is probable that the females at seven trios described by Quinney (1983) also misplaced parental care due to the close hatch dates at his nests, mixing of broods, and an assumed inability of parents to recognize their own young. Females from these trios also had lower reproductive success due to the disappearance of young and eggs from trio nests. Nesting-trios in Tree Swallows apparently occur under conditions of extreme nest-site limitation and good habitat quality, but because of the drawbacks of trio-nesting, it is not surprising that female Tree Swallows aggressively defend nest-sites from floating females (e.g., Stutchbury and Robertson 1987, Dunn and Hannon 1991), and that trios of Tree Swallows are uncommon in both nest-box and natural populations.

The SY female repeatedly oscillated between mature adult reproductive behavior (i.e., caring for young) and the behavior of a nest attendant (i.e., stealing food), indicating that Tree Swallows can quickly switch between the typical roles of a breeder and non-breeder during the nesting season. Lombardo (1986, 1987a, b) showed that many attendants at Tree Swallow nests were mature, non-breeding birds that were exploring potential nest-sites for future breeding attempts. These attempts may occur within a season, or in subsequent seasons. Ultimately, all mature Tree Swallows are driven to breed each year, but under some conditions the benefits from doing so may be relatively low, such as those associated with nesting in polygynous trios. Maintenance of control over breeding drive based on proximate environmental cues (e.g., nest-site availability), and an associated flexibility in behavioral roles, might be favored by selection in nest-site limited species such as Tree Swallows (Holroyd 1975, Rendell and Robertson 1989) because it would allow individuals to abstain from nesting under poor environmental conditions, but swiftly occupy any good nesting opportunities that arise.

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Wallace B. Rendell, *Behavioral Ecology Research Group, Dept. of Biological Sciences, Simon Fraser Univ., Burnaby, British Columbia V5A 1S6, Canada.* *Received 17 Oct. 1991, accepted 29 April 1992.*

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A nest and egg of the Rufous Antpitta in Ecuador.—The nesting habits of *Grallaria* antpittas are poorly known owing to the dense understory vegetation frequented by most of the species and the generally secretive nature of the birds. This note provides the first description of the nest and egg of one of the common species, the Rufous Antpitta (*Grallaria rufula*). On 25 March 1990 I found a nest of a Rufous Antpitta at about 2700 m in the valley of the Rio Chalpi Grande approximately 9 km by road east of (below) the town of Papallacta (0°22′S, 78°08′W; Paynter and Traylor, Ornithological gazeteer of Ecuador; Cambridge, Massachusetts, Harvard Univ. Press; 1977) on the east slope of the Andes in Napo province, Ecuador. The river valley and surrounding region is heavily forested although some large patches of forest have been cleared along the road and on nearby mountain slopes. The nest was situated in lightly disturbed forest (many of the largest trees had been removed) with a dense, woody understory dominated in places by *Chusquea* sp. bamboo (although bamboo was not dense at the nest site). Walking along a trail contouring a steep slope about 30 vertical m above the rushing river, I first noticed the motion of a bird sneaking away downslope through the undergrowth. On inspection, I found a Rufous Antpitta sitting quietly on a thin horizontal branch about 1 m above the ground. The bird sat motionless for more than 2 min only about 6 m from me, and I suspected that it had a nest nearby. After some searching, I located the nest in the side of a large, moss-covered stump about 1.5 m tall, well hidden from outside view by dense surrounding vegetation. The nest appeared to be sunken into a shallow hollow in the side of the stump, about 0.75 m above the ground. A part of the stump formed an overhang above the nest, and small herbaceous plants about 15 cm tall growing out of or immediately beside the rim of the nest, one on either side, concealed the nest even at close range.

I did not have a ruler with me at the time, but from marks made on a piece of paper and later measured, the nest was about 9 cm wide from rim to rim across the cup, and the cup was steep-sided and about 5 cm deep in the middle. The rim of the nest consisted entirely of thin, yellowish grass stems and the cup was lined with what appeared to be 30–40 yellowish mammal hairs, each about 4 cm long. The bottom of the cup was visible through the lining, and seemed to be made of dark, damp leaves. The nest held one egg. It was an even, turquoise color, close to the color of a typical egg of the American Robin (*Turdus migratorius*), but slightly duller, thus similar to the color of the few known eggs of other species of *Grallaria* described to date, with the notable exception of *G. ruficapilla*, which has buffy eggs with rufous blotches (Wiedenfeld, Wilson Bull. 94:580–582, 1982). I did not measure

the egg, but estimated that it was a little less than 2.5 cm (1 inch) long and noted that the small end was rather rounded and not much smaller than the large end. I left the nest undisturbed. When I passed by again about an hour later the bird flushed from the nest as before, by quietly sneaking away on thin limbs within 1 m of the ground to stop a few m downslope. I was not able to make further observations on the nest until 1 April, when I found that the adult Rufous Antpitta was still incubating and the nest still held only one egg. Wiedenfeld (1982) reported that the normal clutch size in Grallariinae (sensu Lowery and O'Neill, Auk 86:1–12, 1969) is two. In light of the fact that the bird had been actively incubating for at least a week without laying a second egg, my observation appears to represent a single-egg clutch. Although it is possible that another egg had been laid in the last week of March followed by the disappearance of one by 1 April without causing nest abandonment, this seems an unlikely set of circumstances.

Although there are no other direct observations of breeding behavior of *G. rufula,* Hilty and Brown (A guide to the birds of Colombia; Princeton, New Jersey, Princeton Univ. Press; 1986) reported that five birds collected March to May in the Perija and Santa Marta mountains of northeastern Colombia were in "breeding condition." Of seven specimens (5 males, 2 females) collected 13–23 Mar 1992 in Carchi Province, Ecuador (3100 m on the west slope of the Andes) by the Academy of Natural Sciences Philadelphia, are all in breeding condition (M. Robbins, pers. comm.). Size of the largest ovum of these females (1 mm and 2 mm, which is considered small) indicated to Robbins that the birds had either recently laid eggs or were just coming into breeding condition, although he suspected the former, stating that it is not possible to determine for sure without knowing the size of the oviduct (M. Robbins, pers. comm.). These data correspond well with my observations. Data on size and condition of gonads of numerous specimens from the northern half of Peru collected between June and October (no specimens available for other times of year; G. Graves, pers. comm.) suggest that breeding activities commence around early to mid-September in that part of the species' range.

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Bret M. Whitney, *Field Guides Incorporated, P.O. Box 160723, Austin, Texas 78716-0723.* *Received 12 Feb. 1992, accepted 1 June 1992.*

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ORNITHOLOGICAL LITERATURE

HOMEWARD BOUND: PROBLEMS WADERS FACE WHEN MIGRATING FROM BANC D'ARGUIN, MAURITANIA, TO THEIR NORTHERN BREEDING GROUNDS IN SPRING. B. J. Ens, T. Piersma, W. J. Wolff, and L. Zwarts, eds. Special Edition of Ardea 78 (1/2), 1990: 364 pp. No price given.—The Banc D'Arguin is a tidal, shallow section of the Saharan Atlantic coast of Mauritania that is a major wintering area for Palearctic, and to a lesser extent Nearctic, breeding shorebirds. This book, originally published as a special edition of *Ardea,* is a collection of 23 papers by 11 senior authors, two of whom (Zwarts and Piersma) account for 40% of senior authorship. All senior authors are from the Netherlands, where vast numbers of shorebirds gather at major migration staging areas on the Wadden Sea coast, many of which continue migration to wintering areas on the West African coast.

The editors have grouped the papers, all of which are original works, into topics addressing basic shorebird migration and wintering ecology, this as a way of appraising conservation needs from a sound biological perspective. The book divisions address questions of (1) why the Banc D'Arguin is so attractive to shorebirds, (2) migration patterns of shorebirds wintering there, (3) migration behavior, and (4/5) two sections dealing with energetic aspects of migration.

The papers of the first section raise as many questions about why so many shorebirds winter at Banc D'Arguin as they answer. An obvious hypothesis would be that there is an unusual availability of food, an idea not supported by earlier research or by research of the papers in this work. The Banc D'Arguin evidently has a relatively low annual biomass production as compared to temperate sites. The studies which look at food and foraging are observational studies of feeding birds. Zwarts et al. found that prey taken by small shorebirds tend to be much smaller than at sites studied in Europe; unfortunately, the sampling design had not anticipated this. Due to problems of identifying prey, more emphasis is given to the largest species such as curlews, godwits and oystercatchers whose prey populations were reliably determined, leaving open questions about foraging of many of the smaller species which comprise the majority of shorebirds wintering at Banc D'Arguin. The tentative explanation of why so many shorebirds winter at Banc D'Arguin hinges on the size of prey consumed by the smaller species, which could not be determined. Unfortunately, potentially supporting data, for example from stomach contents of birds accidentally killed, and/or from invertebrate sampling and exclusion cage studies, was not described.

Part 1 also includes preliminary studies of other factors of shorebird wintering ecology such as heat stress (not indicated) and salt stress (differs among individuals, depending on opportunities for acclimatization, and among species), and the possibility of synergistic stress from salt and heat. Finally, part 1 includes a paper by Bijlsma on the predatory behavior of falcons on shorebirds. Falcons concentrated their hunting on the high tide resting areas of shorebirds, especially in the case of Dunlins (*Calidris alpina*) taking mostly juveniles.

Part 2 focuses on the geographic origins and migration patterns of shorebirds wintering at Banc D'Arguin. Much of the potential underlying these studies depends on the breeding ground geographic variation of the species involved, as well as on the availability of comparable biometric data from sites used for comparison, for example the Netherlands and the United Kingdom. Comparative data also were available from Guinnea-Bissau and South Africa. A wealth of information is available, and convincing evidence is presented by Wymenga et al., to show that shorebirds wintering at Banc D'Arguin come from western Nearctic breeding grounds (e.g., Sanderling [*C. alba*]) to as far east as Siberian breeding grounds (e.g., Red Knot [*C. canutus*]). For some species they also found indications that birds wintering in Guinnea-Bissau were from breeding zones farther north and east than for counterparts

caught at Banc D'Arguin. Considering all species together, three general patterns were evident: (1) species which breed in the Baltic, Fenno-Scandinavian, and Western or Central Siberian area, (2) those migrating principally to Iceland/Greenland, and (3) exceptions to these which generally have eastern breeding distributions. The clear, graphic species by species summaries used by these authors are especially noteworthy.

In their paper, Zwarts and Piersma conclude that the Banc D'Arguin also is an important migration staging area for shorebirds that winter farther south than Mauritania. The authors note that evaluations were complicated by not knowing whether counts made at high and/or low tides were most appropriate for analysis and by not knowing migration arrival/departure dates at key sites to the south such as at Guinnea-Bissau. Evidently many birds in transit visit Banc D'Arguin but do not necessarily accumulate fat there.

Piersma et al. describe spring migration departure of shorebirds from Banc D'Arguin based on three years of data on visible departures. While visible, departing waders typically ascend to altitudes exceeding 1.5 km. Species' departure dates are correlated with nesting latitudes, with more northerly breeders departing on later dates. Most species showed unimodal departure dates, with no evidence suggesting that departures are correlated with surface wind conditions.

Using information on biometrics, mass change, turnover, and band recoveries, Goede et al. evaluate spring migration of Dunlin departing the Dutch Wadden Sea. They develop persuasive evidence to suggest that two distinct groups of Dunlin use the staging area, one in April and early May that breeds in northern Europe and another during late May that breeds in Siberia. They suggest that both groups winter principally in Great Britain and along the Atlantic coast of Europe.

Van Dijk et al. report on shorebirds summering on the Banc D'Arguin and show that roughly 16% of wintering numbers remained at Banc D'Arguin during Boreal summer; their distribution corresponded well with winter distribution at Banc D'Arguin. The authors suggest that most summering shorebirds are younger than breeding age.

The third section of "Homeward Bound" is comprised of two papers which focus on behavioral aspects of migration. In an especially interesting paper, Piersma, Zwarts, and Bruggemann present a comprehensive evaluation of flocking behavior, including flock size and formation, vocalizations, orientation, flight speed, and flock ascent. Most of the study is based on observations from Banc D'Arguin, but additional information about departures in Europe during spring and autumn is included. Size of departing flocks was typically lower than of resting flocks or flocks in local movements. Larger than average departing flocks tended to split into smaller flocks, and smaller than average flocks often merged into larger flocks. There was a tendency for larger species to form larger flocks. Mixed species flocks were uncommon, and when they formed, companion species generally were of similar size. Also discussed is behavior of embarking flocks, ascent rates, departure tracks with respect to wind (compensation is not indicated except during following winds), diurnal timing (most departures were during afternoons), and cloud cover at departure (sun always visible). This paper and its discussion should be considered imperative reading by students of flocking.

The second paper, by Blomert, Engelmoer, and Ntiamoa-Baidu looks at the Banc D'Arguin as a briefly visited meeting point for migrating Avocets (*Recurvirostra avosetta*) departing from sites south of Banc D'Arguin. The fact that arriving flocks are smaller than departing flocks, and that the arriving flocks are smaller than flocks departing Guinnea-Bissau to the south, suggests to the authors that the brief visits of Avocets at Banc D'Arguin are useful for the reformation of flocks that have become disorganized.

The papers of the fourth section explore energetic aspects of preparation for long-distance migration by shorebirds. Zwarts and Blomert's paper evaluated the food value of crabs eaten by Whimbrels (*Numenius phaeopus*), exploring how energy intake may be maximized. High

ingestion rates (much of it indigestible) reduces digestibility. Still, net energy accrued is greater with high crab consumption. Bottom line: captive Whimbrels needed to increase food consumption by 45% to realize a 30% increase of digested energy.

Klaassen, Kersten and Ens used captive shorebirds to look at maintenance and premigratory fattening energetics, focusing especially on comparisons between shorebirds wintering in tropical versus temperate regions. The work indicates that temperate-wintering shorebirds have maintenance metabolic rates averaging 42% higher than tropical-wintering shorebirds. When tropical-wintering Ruddy Turnstones (*Arenaria interpres*) were displaced for one year to the Netherlands, the authors note that "It is thrilling that the results of this 'control' experiment . . . reproduce the original discrepancy . . . ," raising fundamental questions about the underlying mechanisms regulating metabolism.

Piersma and van Brederode continue with their study of pre-migratory fattening, focusing on relationships between body size versus fat and non-fat mass. They quantify the proportions of pre-migratory mass increase that is attributable to fat deposition versus non-fat mass change. In the four species with sufficient sample sizes, pre-migratory mass increase consists of 55–75% fat, with the balance being mostly muscle increase.

Zwarts, Blomert, and Hupkes looked at foraging behavior of shorebirds at Banc D'Arguin during the 4–6 weeks before migration departure. The species they studied did not increase feeding time during daylight, which is restricted by tidal flux. However, in 10 of 14 species, the feeding activity increased during times of tidal flats immersion. In addition, nocturnal feeding of several—but not all—species increased during March and April, especially on 'light' versus 'dark' nights. In related evaluations, the authors found a negative relationship between average body mass of species and their diurnal feeding activities. Likewise, smaller species tended to feed more at night than larger species; they note, however, that several complications could affect their conclusions. Chief among these is that digestive bottlenecks (see below) could explain different foraging times of small versus large species and that no data allowed comparing effectiveness of foraging under different (day/night, tactile/visual) conditions.

Zwarts and Dirksen studied digestive bottlenecks in free-living Whimbrels, and showed that maximum food assimilation is not merely a function of food intake, but also of the ability of the digestive tract to process food. Even though per unit time intake is greatest during pre-migration, increased consumption also is achieved by expanding foraging hours. Increase may also be facilitated by discarding less digestible parts of crabs. In a stimulating discussion, the authors suggest that Whimbrel at Banc D'Arguin are living at their physiological limit, even during the winter. In the paper following this one, Zwarts suggests that pre-migratory fattening of Whimbrels at Banc D'Arguin is possible only because of a seasonal increase of available resources, caused in good part by changing activity patterns of the Whimbrels and of their marine crab prey. Moon phase played a role in the crab/Whimbrel activity patterns, and migratory departures also appeared related to moon phase.

The last section of "Homeward Bound" evaluates energy budgets of alternative migration schemes. The first paper, by Ens et al., should be read by people undertaking shorebird banding projects, for it contains a wealth of suggestions regarding field methodology as well as evaluation of data. Their work indicates that many adult Ruddy Turnstones from Mauritania migrate to Greenland/eastern Canada whereas others migrate to Fenno-Scandinavian breeding zones. Young birds (ca one year old) do not migrate.

Piersma and Jukema's stimulating paper assesses the migration energy budget of Bartailed Godwits (*Limosa lapponica*) in their highly synchronized migration between the Banc D'Arguin and their next migration staging areas on the Dutch Wadden Sea. Although the authors assemble evidence to suggest that the Banc D'Arguin godwits are among those studied in the Wadden Sea, I did not find the case to be compelling.

Godwits at the Banc D'Arguin show steadily increasing masses beginning in March. The rate of mass gain at the Banc D'Arguin was roughly half that gained at the Wadden Sea. Roughly half of this mass gain was attributable to fat deposition, which provides roughly 90% of the available migration energy, with the balance being non-fat tissues, mostly muscle protein. Taking wind into account, the authors estimate flight distance capabilities of godwits based on their empirical observations of mass change between the godwits at Banc D'Arguin and those at the Wadden Sea. They then compare these observations to various formulae designed to estimate flight distance capabilities, with some unexpected results, especially with respect to those prior formulae which factored in components of wing morphology to derive flight distance capability estimates. The empirical estimates from this study fall between the lowest and the highest theoretical estimates. The authors conclude that godwits from the Banc D'Arguin do not have much of an 'energy margin' in making their flight between West Africa and the Wadden Sea.

Zwarts et al. close out the volume by looking at molt and body conditions of shorebirds just prior to departure from Banc D'Arguin, especially focusing on questions of whether the accumulated evidence indicates that different migration strategies are employed by shorebirds wintering at Banc D'Arguin. They point out that there is a wide spread of spring migration departure dates at Banc D'Arguin, both within and between species, excepting Bar-tailed Godwits. Species breeding in temperate regions migrated earlier than Arctic-breeding species. Prenuptial molt in all species was completed about four weeks prior to migration departure, suggesting the two processes are physiologically linked.

The authors also look at relationships between departure mass of shorebirds and their winter (lean) mass, showing that the larger the species (e.g., Whimbrel, Bar-tailed Godwit) the lower is the migratory reserve as a percentage of body mass. They also looked at mass gain as it relates to incipient migration distance. In their words, "As we see it, departure mass is adapted to the travel distance and the rate of mass gain to the average feeding conditions. These two bear no relation to each other, so we were surprised to see that the higher the departure mass, the faster the rate the mass is deposited." This would appear to be a fruitful area of future research.

The collection of papers in "Homeward Bound" is "must" reading for anyone working on shorebird nonbreeding biology, and for anyone working on more general topics of migration ecology; it contains a wealth of stimulating ideas as well as a large volume of sound, factual information.—Brian A. Harrington.

The Known Birds of North and Middle America, Part II. By Allan R. Phillips. Publ. by author, Denver, Colorado. 1991: 249 + liii pp., 5 color plates, 5 range maps, 8 taxonomic keys. $64.—This book describes species and subspecies-level taxa "known" by Phillips and some of his colleagues (D. D. Gibson, K. C. Parkes, M. A. Ramos, and A. M. Rea) in the Bombycillidae, Sylviidae, Muscicapidae, Prunellidae, Motacillidae, Sturnidae, and Vireonidae. The Introduction includes sections on biodiversity, can we trust our eyes, more on sightings, statistics versus perception, the new Dark Ages, and lessons of *Catharus* thrushes. The main body of the book includes species and subspecies accounts and taxonomic keys.

Although the introduction reads like a tract from the Creationist literature, and rambling would be a kind description for parts of it, Phillips makes many points with which we agree. For example, we agree that far too little emphasis is placed on collecting specimens, the importance of systematics, and funding of biological inventories. We share his concern about the prevalence of anti-collecting attitudes and the lack of documentation given by the AOU Check-list committee for some of their pre-1984 actions. We agree that phenotypic variation in North American birds is known incompletely (having already said so in Zink and Remsen,

1986, Current Ornith. 4:1–69) and that too few people study it. We also agree that some papers are obfuscated with extraneous statistics and that some studies using molecular methods contain a bewildering array of measures of genetic variability. However, Phillips fails to realize that not everyone is interested in the narrow topic that he is (variation in the external phenotype). Systematic biology is now a broad and exciting field that incorporates many endeavors, some of which Phillips neither understands nor appreciates.

Given that Phillips discounts "modern" (=molecular, statistical, or both) avian systematics, what does he offer instead? His methods are vague at best: specimens examined are not stated and his characters are often loosely defined and highly subjective. Because his analyses (=subjective comparisons) lack rigor, we doubt that anyone could replicate his studies and arrive at the same conclusions. His abhorrence of quantitative analysis means that we cannot tell whether his taxa are really distinct, products of incomplete sampling, or arbitrary partitioning of clines. We found his description of his research program telling (p. xliv) "I persist in considering taxonomy the *art* (italics ours) of judging relationships. . . ." It should come as no surprise that this "science" failed to attract many students to systematics or to earn respect of other scientists. It cannot escape notice that attention in ornithology shifted away from systematics during the description-of-subspecies era in which Phillips was trained. The current "revival" in avian systematics is because new techniques and ideas were incorporated into this area of research. Phillips, however, has not incorporated many new methods or ideas into his research, not that that is always necessary for obtaining new information. Most systematists agree that important theoretical and methodological contributions have been made to the field, including the study of geographic variation and species limits. For example, studies of geographic variation are now mostly quantitative and the results often interpreted in an evolutionary rather than strictly taxonomic context; Phillips seems to resent this trend, but he has no scientific reason for this view. The use of statistical methods in documenting geographic variation is widely established, and it is, therefore, hard to find credibility in Phillips' view that statistics were introduced into systematic ornithology as a "crutch for weak subspecies." That Phillips does not recognize geographic variation as an inherently statistical concept is astonishing. Statistical analyses, as well as molecular genetic methods, have all contributed to the resurgence of interest in the analysis of geographic variation and its evolutionary significance. This is not to say that description of taxa based on morphology is not valuable, but quantitative methods represent a drastic improvement over subjective, verbal descriptions.

What is the justification for modern analyses of geographic variation? One concern of such studies is the detection of basal evolutionary taxa or phylogenetic species. Clearly, such basal groups evolve via a restructuring of the genetic variation within populations. Phillips considers genetic variation the underlying cause of the geographic variation in morphology that he partitions taxonomically. Genetic variation within populations is converted to among populations on the breeding grounds, and it is here that modern students of geographic variation collect their specimens. However, Phillips continually stresses the need for "fresh fall specimens" because their plumages are not worn, and because they permit better assessment of colors. Unless specimens are clearly from a known breeding population they are *irrelevant* for analyses of geographic variation. Anyone using fall specimens should have first banded them on the breeding grounds to establish their true breeding area (even sedentary species exhibit post-breeding dispersal). Many students of geographic variation have switched to other character sets, such as skeletal measurements, which can be studied irrespective of degree of feather wear in specimens taken from breeding populations. For the type specimen of *Catharus fuscescens levyi* subsp. nov., Phillips used a fall TV-tower-killed, immature male from Wisconsin. Because the description of this new taxon was not based on careful study of variation among breeding populations, we urge that it not be

accepted. Acceptance of such taxa would be akin to advocating a return to typological thinking.

Despite the theoretical and methodological limitations of Phillips' approach, and his distracting ramblings and personal attacks (as in Part I, research from persons at Berkeley is dismissed), we think his summary of specimens of North American birds is useful. Anyone interested in geographic variation of a taxon discussed by Phillips should consult his species accounts. Forty-five new subspecies (most with primarily Mexican distributions) are described in this volume. However, the new taxa are diagnosed primarily by slight color variations and some might be arbitrary divisions of clines. Independent corroboration of the new taxa with the same and other character sets must precede their acceptance. Clearly, Phillips' subjective assessments might encourage further research and lead to the discovery of undescribed phylogenetic or biological species.

The species accounts update distributional information and are useful for subspecies' distributions. Obviously, Phillips has invested considerable effort into locating specimens relevant to his distributional analyses. However, a quick check of our specimen holdings (examined several times by Phillips) of North American *Catharus* (and *Hylocichla*) thrushes resulted in the following omissions from the species accounts: *C. fuscescens* (winter record, 18 December 1983, Cameron, Louisiana, and presence of Louisiana late spring migrants to 31 May [1], 5 June [2]); *C. guttatus oromelus* (the only record for E. USA, 29 April 1984, Cameron, Louisiana—identification by Phillips); *C. minimus* (specimens to 6 June); *C. ustulatus swainsoni* (account does not indicate that its winter range is mainly lower montane Andes); and *Hylocichla mustelina* (two Louisiana specimens taken in February). We suggest thorough examination of his other species accounts.

Phillips is skeptical of sight records by all but himself and a few friends, and defends their omission by citing old and long-recognized examples of erroneous records being published. A section on Dubious and Erroneous reports is contained in many accounts and offers Phillips' views on specific sight records. Unfortunately many of the sources that Phillips used are omitted so as "to . . . not . . . bore the readers with citations." This hardly advances the science of avian distributions. Likewise, disregard of acceptable sight records results in incomplete distributional information. For example, in Part I (p. 82–83) the resident population of Chestnut-backed Chickadee on the west slope of the Sierra Nevada was omitted, apparently because there were no specimens, in spite of the zoogeographic and ecological significance of the recent colonization of this area. However, we do agree that if possible, specimens are preferred over sight records, because of the wealth of additional information that specimens provide.

Keys are provided for species identification of some genera (e.g., *Catharus*) and are relatively useful, especially if a reference series is at hand. The color plates provide an aesthetic break to the text, but are of little value. The *Catharus* painting (plate 2) is a poor rendition, especially considering Phillips' concern with accuracy and his view that illustrations in recent field guides inhibit proper identification. Plate 3 is supposed to illustrate a typical "western" Veery, which Phillips claims resembles a Swainson's Thrush, thereby showing that field identification is tenuous. However, the Veery specimen selected does not seem representative of a typical Veery (of any subspecies). None of the 32 recent (1981–1991) Veerys (primarily *C. f. salicicola,* a few brighter individuals of eastern subspecies included) in our collection approaches this individual in the buffiness of the face (especially around the eye) or along the flanks. The plate (No. 5) depicting subspecies of Warbling Vireo might illustrate the subtle plumage differences of the southeastern taxa (subspecies to Phillips), but there is no discussion of these characters in the figure legend. Because Phillips makes numerous caustic comments about the lack of accuracy in the work of modern ornithologists, we note that the leg color of the Warbling Vireo is leaden blue, not flesh, as illustrated.

If Phillips completes his series, will it be the best reference for avian distributions? Actually, given the fluid nature of bird distributions, we question whether there is such a thing as a "best" source of distributional information. Because Phillips does not consider most sight records, we suspect that his descriptions of ranges will be less useful than those that incorporate carefully evaluated sight records. However, his criticisms of many sight records should be taken seriously.

We suggest that persons interested in intraspecific variation will want to consult Phillips' species accounts. Those interested in distributions would be just as well off combining general and regional references for the species in question.—Robert M. Zink and Donna L. Dittmann.

Conserving Migratory Birds. Edited by T. Salathé. ICBP Technical Publication No. 12, International Council for Bird Preservation, Cambridge, U.K. 1991: 405 pp. (British pounds 19.50).—Migratory birds have been receiving increased attention lately. In the United States, an ambitious Neotropical Migratory Bird Conservation Program for the western hemisphere has been launched that involves a partnership of Federal and state agencies, nongovernmental organizations and academic ornithologists. Globally, the International Council for Bird Preservation (ICBP), which has been in the forefront of migratory bird conservation since its founding in 1922, has now made migratory birds the focus of its twelfth technical publication.

Migratory birds differ from other avian groups of concern in that relatively few species of long-distance migrants are endangered. According to ICBP, only 106 (10.3%) of the 1029 globally threatened species of birds are long-distance migrants (it is a sad sign of the times when one uses "only" to refer to 106 species of threatened birds). According to Jean-Pierre Biber and Tobias Salathé, most of the threatened migrants depend upon wetlands (41%) or are seabirds (26%). However, as ICBP Director-General Christoph Imboden points out in his foreword, "investigations in North America and Europe suggest that there is hardly a migratory species that, during the past 20 years, has not declined in numbers." We are thus faced with a "slow erosion" of abundance and distribution of widespread species, which is perhaps the least discussed aspect of the global loss of biodiversity.

"Conserving Migratory Birds" grew out of a 1989 conference of ICBP's European Continental Section. As a result, it deals disproportionately with the Western Palearctic and African flyways; more than half of the 23 papers deal with the Old World. The book is not intended to be comprehensive; its purpose is to illustrate specific problems and solutions. The introductory chapter by Salathé, the editor, describes the ICBP Migratory Birds Conservation Program, which he coordinates. The remainder of the book is divided into three sections: Problems Facing Migratory Birds, Conserving Migratory Birds, and Future Directions. Most chapters present case studies of specific conservation projects, with significant socioeconomic and legal components to many chapters. There are also overviews of regional situations, chapters on legal instruments such as the Bonn Convention for the Conservation of Migratory Species of Wild Animals, and an excellent paper by B. A. Lane and D. Parrish that summarizes the Asian-Australian bird migration system.

Unevenness is the hallmark of this publication. Although most chapters are well documented, others are anecdotal. The rationale for inclusion of papers is unclear. In particular, the section on problems facing migrants lacks balance. Despite the statement in the overview chapter that "alteration and destruction of natural and semi-natural habitats are *the* major threats" to birds worldwide (p. 22), two of the three case studies in this section deal with hunting, and the third discusses the impacts of pesticides.

The collection includes three papers with a New World focus—overviews of federal re-

search on conservation of nongame migrants in the U.S. (Marshall Howe), migrant birds in neotropical forests (John Rappole), and the Western Hemisphere Shorebird Reserve Network (Laurie Hunter et al.). The Old World tilt of the rest of the book is, in fact, useful to the American reader. We learn that in contrast to our (misplaced?) focus on forest birds, European birds of open habitats—grasslands and wetlands—are at greatest risk. Most of these birds migrate across the Mediterranean Sea and the Sahara Desert (where some passerines may stop to rest but not feed). The Mediterranean *maquis* between the sea and the desert is thus a critical habitat. Once across the Sahara, the birds of the western Mediterranean flyway winter mainly in the Sahel, where they must contend with drought and the literally hundreds of millions of people who themselves face not only drought, but malnourishment and potential starvation.

The case studies feature the roles that nongovernmental conservation organizations play in Mali, Turkey, Malta, Ghana, Nigeria, Japan, and Taiwan as well as in Europe. The common ingredient in all these programs is an integrated approach to conservation and economic development with a strong emphasis on education. Two approaches to bird conservation are presented. The traditional approach involves establishment of protected areas for populations that are concentrated around scarce resources (such as wetlands) and other key migratory stopover or wintering sites. However, this strategy does not work for species that are distributed widely as is the case for most migrants.

In the penultimate chapter, Patrick Dugan of the World Conservation Union (IUCN) calls for a new approach which features conservation and sustainable development in Africa. His message is that "rather than focus directly on the problems facing individual species . . . , conservation efforts may therefore be made more effective by addressing the diverse social and economic problems which are putting pressure on those natural ecosystems upon which migratory birds depend" (p. 375). He points out that in migrating between Europe and Africa, birds move back and forth between wealthy countries with wealthy farmers and strong national governments and private groups that support conservation and poor countries with impoverished, hungry farmers who largely view birds as pests, competitors, or a food source and where conservation is often seen as being in opposition to development. He argues that in the process of building environmental awareness, it "will not always be necessary or advisable to stress birds."

The volume concludes with Salathé's presentation of ICBP's action plan for the Western Palearctic and African flyways. While the work of ICBP will certainly continue to focus on birds, it is encouraging that their educational objective is expanding to include greater emphasis on awareness of the linkages between the well-being of birds and of the human populations that depend upon the same ecosystems. ICBP is also evaluating the impact of development assistance programs on migratory birds and their habitats. Inasmuch as conserving migratory birds entails fighting poverty and inequity, ICBP and its colleagues have barely begun their work.—David E. Blockstein.

The Mountain and the Migration: A Guide to Hawk Mountain. By James J. Brett, illus. by Frank Fretz and Frederick Wetzel. Cornell University Press, Ithaca and London. 1991 (revised and expanded from 1986 ed.): xii + 114 pp., 17 black-and-white plates, 13 black-and-white photographs, 13 unnumbered figures and tables. $12.95 (paper).—Few locales in North America have been the subject of as many renowned publications as Hawk Mountain, Schuylkill County, Pennsylvania. Following the path blazed by Maurice Broun's *Hawks Aloft* (1948) and Michael Harwood's *The View from Hawk Mountain* (1973), James

Brett's revised and expanded guide to Hawk Mountain provides a useful summary of historical information presented in those two works, as well as a fine introduction to the geology and natural history of this site, with emphasis on the hawks migrating past the lookout each autumn.

Anyone planning a visit to Hawk Mountain will be enriched by reading Brett's guide. However, the work has broader application than that. Its contents may be used to understand better the geologic forces that created, and the natural communities that inhabit, almost any ridgetop site in northeastern North America. Furthermore, the guide offers a good summary of the dynamics of hawk migration. Finally, and perhaps most importantly, it provides an excellent discussion of information used to identify northeastern hawks in flight, as well as fine black-and-white plates depicting these species in a variety of poses and plumages.

Even though the hawk identification material may be the most important, and is certainly the best presented information in this book, it is not without fault. Without wishing to diminish the achievement of Brett's work, let me note a few, mostly minor, matters that deserve correction in future editions. First, and by no means a minor matter, the plates of the hawks are not in color. Any neophyte attempting to learn hawk identification would do well to begin with a series of color plates in one of the field guides (preferably Clark's "Hawks") before graduating to Wetzel's well-presented black-and-white drawings. As a result of this deficiency, one of the primary purposes of the guide—to act as an introduction to the various topics discussed, including hawk identification—is inadequately fulfilled. I realize that cost considerations probably dictated that plates in this guide not be in color, and I also realize that hawk identification involves many matters that have nothing to do with the color of birds of prey, but these plates will undoubtedly never be the place where beginners start learning hawk identification as long as they lack color. I hope that some future edition of this work will remedy this deficiency, because the plates are otherwise a wonderful presentation of field marks for the identification of hawks. I was especially pleased by the "head-on" and "tuck" profiles offered for most of the hawks; head-on profiles for Merlin (*Falco columbarius*) and Gyrfalcon (*F. rusticolus*) are, incidentally, lacking. Additionally, the difference in the streaking of immatures of Cooper Hawks (*Accipiter cooperii*) and Sharp-shinned Hawks (*A. striatus*) is not well presented.

The text opposite each plate discusses identification of the species and is quite thorough and up-to-date. I detected only a few matters of concern. I do not believe, for instance, that it is accurate to state that "there is little difference between adults and immatures" of Swainson's Hawks (*Buteo swainsoni*); there is certainly enough difference, especially in the more common light-phase birds, to warrant inclusion of a drawing of the immature, particularly if Brett is right in suggesting that Swainson's Hawks "may have been undercounted" at Hawk Mountain in the past. Also, Brett might mention the conspicuous light flecking found on the dorsal plumage of immatures of the Osprey (*Pandion haliaetus*), as well as the tendency of females and immatures of Northern Harriers (*Circus cyaneus*) to have a much darker underwing inward from the alula rather than outward.

The "Suggested Reading" section lacks mention of Ralph Palmer's monumental "Handbook of North American Birds" (Vols. 4 and 5: Diurnal Raptors); these volumes contain a wealth of information about the migration and identification of the hawks migrating past Hawk Mountain. Brett might also use the term "raptor" less loosely in future editions; it includes nocturnal birds of prey as well as diurnal ones. Finally, I would like to see capital letters in the common names of the species used (or not used) consistently.

Almost anyone who studies hawks will benefit from reading this book. All those who watch hawks for pleasure or science in the eastern United States will want to own a copy. It is a fine addition to the works devoted to Hawk Mountain.—Stephen J. Stedman.

Seabird Status and Conservation: A Supplement. J. P. Croxall, ed. International Council for Bird Preservation, Technical Publication No. 11, Norwich, U.K. 1991: 316 pp., 64 maps, 41 tables. £17.50.—This collection of 15 papers documents the status of and threats to seabird populations in geographic areas which were omitted, or covered superficially, in ICBP's 1984 volume "Status and Conservation of the World's Seabirds." Each paper summarizes information on the abundance and distribution of seabird populations as well as indicating where gaps in current documentation occur. Additionally, each chapter outlines principal threats to seabirds in the region, existing conservation actions, and suggests methods of meeting conservation needs. In format, this work follows the style and depth of treatment accorded to geographic regions in the original volume.

Four of the papers present new data for regions covered in the previous volume where conservation problems have intensified during the last five years: California, Indonesia, and the northeast and southeast coast of the former Soviet Union. The majority of the work is given over to presentations on regions not previously discussed: northeastern and northwestern Canada, Baja California, the Great Lakes, Brazil, Uruguay, Sri Lanka, Malaysia, the Marianas, Heard and McDonald islands, and the Australian segment of the Antarctic continent.

This volume goes far in filling the gaps in coverage of regions important to seabirds but leaves several prime areas (such as New Guinea, Argentina, India, Micronesia and Melanesia) to be treated at a future date. The species covered are penguins (Sphenisciformes), albatrosses and petrels (Procellariiformes), boobies, frigatebirds, tropicbirds, cormorants and pelicans (Pelecaniformes), skuas (Stercorariidae), gulls and terns (Laridae), skimmers (Rynchopidae), and auks (Alcidae).

Problems common to many regions include loss of habitat, the introduction of exotic predators, direct exploitation of seabird products, deterioration of marine ecosystems, and increased mortality of seabirds as incidental catches in non-selective fisheries. Man, with his capacity to directly or indirectly affect seabird mortality, is implicated in nearly all cases as the principal threat to the continued existence of seabirds. Existing conservation actions to meet these threats generally include habitat protection, buffer zones for oil exploration, research, and protective legislation to curtail direct exploitation. Recommendations for further action frequently mention the need for surveys to determine the impact of human disturbance, monitoring population trends, research into the basic biology of little known species, research on applied methodologies for control of introduced predators, and preservation of habitat through creation of ecological reserves.

The only problem I had with the book (a quibbling detail) is that the Table following the editor's preface contains no heading to aid in interpretation; the purpose of the table, however, is explained in the text. I think that as a companion piece to the first volume, this book is an exceedingly useful tool for scientists, policy makers, conservationists and others who use quantitative information in their decision making.—Justine B. de Cruz.

Birds of the Blue Ridge Mountains. By Marcus B. Simpson, Jr. The University of North Carolina Press, Chapel Hill, North Carolina. 1992: xiii + 354 pp., black-and-white illustrations by H. Douglas Pratt. $14.95 (paperback), $29.95 (cloth).—The volume of visitors to the Blue Ridge Mountains is extremely large, some localities being among the most intensively used natural areas in the United States. Accordingly, there was a need for a guide to finding birds in this area. However, the present book is more than the usual regional guide to finding birds to add to your life list. Simpson has produced a thorough description of many of the trails and localities in the Blue Ridge Mountains frequented by all kinds of

naturalists. Furthermore, he provides introductory comments about a variety of important, associated concerns of the birder. For example, he comments on vegetation and climate as related to birds, choice of binoculars, and possible problems in hiking into remote areas. He provides a specific section on birding for the handicapped and physically impaired. His remarks are insightful and accurate, although I disagree greatly with his observations regarding the extreme scarcity of rattlesnakes. (We have seen a few in and around nearly every campground in western Virginia!)

The text is sprinkled with attractive black-and-white illustrations of various birds. A few maps are provided. These seem accurate, but I would have preferred a bit more detail in these. An annotated checklist of the region is included. This list is useful, although its coverage is uneven. All birders familiar with the area will recognize omissions but probably will learn a few things from the list. Many of the mountains in this range (e.g., Mt. Rogers, Whitetop Mountain, Grandfather Mountain, Clingman's Dome) provide islands of habitat inhabited by birds reminiscent of boreal forests of Canada. Simpson indicates clearly the patchiness of the habitat in these mountains and the associated localization of specific birds. I found the text to be accurate and informative in describing specific areas ("hotspots"), and I am sure that it will be useful to birders new to the region.

This book takes the regional bird-finding manual to a new level. It provides interesting materials beyond where to find birds and is readable just for interest in the Blue Ridge. The book is attractive and nicely bound. I found no typographical errors. The reference section and index to bird species particularly are useful.

I highly recommend this book to both visitors to the Blue Ridge and to "old-timers" who want to expand their appreciation of the area.—C. R. Blem.

The Birds of Australia: A Book of Identification—760 Birds in Colour. Second Edition. By Ken Simpson and Nicolas Day. Tanager Books, Wolfeboro, New Hampshire, 1986: 352 pp. $45.00.—Anyone contemplating a trip to Australia will find this book an excellent identification resource. It is not designed as a field guide as it measures 8.5″ × 11″ and weighs a little over five pounds. In addition to the useful identification section of 271 pages, there is a 70 page handbook which probably would be of little value to most WOS Members. I have taken three extended trips to Australia, and for me it would be the book to have along in the car to check the many identifications which are difficult using presently available field guides.

The organization and page layouts make this book the best I have encountered thus far. The illustrations are large, and the many confusing species which look alike are usually on the same page for comparison. The colors are bright, contrasty, and exaggerated. This could upset purists, but I found these characteristics helpful in easily recognizing the field characteristics that were the greatest help in separating the many "look-alike" species. The illustrations are all on the right and the text for each species is on the left, corresponding closely to the relative position of the illustration of the bird on the right. Each species is clearly numbered, which eliminates any confusion of text with illustrations. On the right margin of the text pages, there is an excellent map showing the distribution of each species. In between the text and the map there are black-and-white line drawings of questionable value. In most cases, the reader would more readily see the same thing shown on the colored illustration page. The unusual nesting site drawings were helpful, but most often these were also illustrated on the color plate.

I feel the greatest weakness in the book is the attempt by the authors to make the book all things to all people. The Handbook portion is so different from what precedes it that it

probably should have been published separately. This would make the book lighter and, hopefully, would reduce the price somewhat, making it more attractive to purchase as an additional resource identification book to carry along in the car. I found it to be the best book to ponder over after returning to camp. The clear illustrations were most helpful in fixing the appearance and names of new species I was learning.—Robert D. Burns.

Illustrations of the Birds of California, Texas, Oregon, British and Russian America. By John Cassin. Facsimile of the 1856 edition. Texas State Historical Association, Austin. 1992: 460 pp., 51 color plates, additional black-and-white illustrations. $29.95; Limited Edition $75.—Except for several species of birds named for him, John Cassin is almost forgotten by present-day ornithologists, and his book is even less familiar. The Texas Historical Association has now published a handsome facsimile copy of this forgotten work.

In 1852 Cassin issued a prospectus for a three-volume supplement to Audubon's "Birds of America" describing those species discovered since the publication of that work. After being issued in parts in 1852–1855, this part of the work was issued as whole in 1856. Poor public response to the work made it impossible for Cassin to complete the contemplated work so only 10 of the proposed 30 parts were published. It is probable that there were never more than a few hundred copies available.

Fifty species are figured in lithographs by Wm. Hitchcock and George White. These vary from poor to almost acceptable by present day standards. Each illustration is accompanied by text of varying length, which includes a description and technical observations, as well more general notes about distribution, behavior, and life history. These accounts make extensive use of quotations from such people as Gambel, Heermann, and other early students of western birds. While some of the information is of use today, the text is mostly interesting as a window into the state of American ornithology in the mid-19th century.

Also scattered throughout the text in no apparent order are several sections entitled "Synopsis of North American Birds." These discuss four orders and six families, and with them Cassin attempted to make a comparison of North American birds with those of the world. As curator of the magnificent collection of the Academy of Natural Sciences of Philadelphia he was the first American ornithologist capable of such a synthesis.

The Introduction by Robert McCracken Peck, of Cassin's home institution, is a biography of Cassin, including the story of the publication of the book. An appendix gives a useful translation of Cassin's nomenclature to that of today.

Thanks to a generous grant from The Summerlee Foundation of Dallas, this impressive example of bookmaking sells for a remarkably low price. It should be of interest to all lovers of fine books as well as ornithological-history buffs.—George A. Hall.

Wilson Bull., 104(4), 1992, pp. 773–789

PROCEEDINGS OF THE SEVENTY-THIRD ANNUAL MEETING

JOHN L. ZIMMERMAN, SECRETARY

The Seventy-third Annual Meeting of the Wilson Ornithological Society was held Thursday, 9 April through Sunday, 12 April 1992 at the Hilton Inn Gateway, Kissimmee, Florida in joint session with the Florida Ornithological Society. The local committee chaired by Dr. Herbert W. Kale II was composed of Brad Andrews, George Becker, Betty Biggs, Reed Bowman, Greg Bretz, Mike Bunn, Bertha Carnahan, Jim Carnahan, Ruth Clark, Buck Cooper, Linda Cooper, Helen Eastman, Jerry Fishman, John Fitzpatrick, Quetta Fouke, Roberta Geanangel, Valerie Gohlke, Ellen Greer, Wendy Hale, Mae Hartsaw, August Hoeger, Stephanie Johnson, David Johnson, Bobbie Kittleson, Peggy Lantz, Rita Levreault, Fred Lohrer, Martha Marshall, Jean Michlewski, Rebecca Payne, Diane Pierce, Lynn Pigg, Helen Ribbe, Parks Small, Susan Smith, Walter Taylor, Trude Valente, Neta Villalobos-Bell, Jan Woolfenden, Glen Woolfenden, Alma Wooley, and Rueven Yosef. The meeting was hosted by the Archbold Biological Station, Florida Audubon Society, Kissimmee Valley Audubon Society, Lake Region Audubon Society, Orange Audubon Society, and Sea World of Orlando.

The Council met from 13:10 to 19:30 EST on Thursday and from 10:45 to 12:00 EST on Saturday. Registration for the 201 guests and members began at 12:00 Thursday in the Orchid Room in The Hilton Inn Gateway, and an informal reception was held that evening. The opening session on Friday convened in the Gardenia Room of The Hilton Inn Gateway at 08:35 where the societies were welcomed by Herb Kale, representing the Florida Audubon Society. President Richard Banks responded for the Wilson Ornithological Society, and Glen Woolfenden responded for the Florida Ornithological Society.

The scientific papers sessions, which included contributed papers and a symposium on Fire as an Ecological Force organized by John Fitzpatrick, were held in the Gardenia and Azalea rooms. Poster papers were presented in the Orchid Room. On Friday evening, Sea World of Orlando hosted a most enjoyable reception at their Penguin Encounter facility, where members and guests encountered not only sub-Antarctic penguins but also alcids, shags, ornithologists, and substantial refreshments. Field trips to local areas were conducted both Friday and Saturday mornings; a half-day's trip, designated Birding the Phosphate Mines, occurred Saturday morning, and Sunday trips rewarded participants with Florida specialities or a visit to the Archbold Biological Station.

The annual banquet was held in the Gardenia Room of the Hilton Inn Gateway, preceded by a social hour on the covered patio where rain showers could not dampen our spirits. After the banquet, the following awards were presented:

EDWARDS PRIZE (for the best major article in volume 103 of *The Wilson Bulletin*) to

Norman P. Hill and John M. Hagan III, "Population trends of some northeastern North American landbirds: a half-century of data." Wilson Bull. 103(2):165–182.

LOUIS AGASSIZ FUERTES AWARD

R. Bruce MacWhirter, "Parent-offspring interactions and the allocation of food in the Northern Harrier."

MARGARET MORSE NICE AWARD

Sharon Lee Milder, "Food and foraging behavior of Christmas Island Warbler (*Acrocephalus aequinoctialis*)."

PAUL A. STEWART AWARDS

Sandra Bos Mikich, "Social behavior and home range of aracaris at a small isolated reserve in north Brazil (Piciformes: Ramphastidae)."

Lourdes Mugica-Valdes, "Feeding ecology of Fulvous Whistling-Ducks."

Jeffrey David Parrish, "Habitat selection by neotropical migratory passerines during the migratory period in New England."

Howard J. Weinberg, "Wood Thrush (*Hylocichla mustelina*) breeding success in small forest fragments: the influence of area and urbanization."

Mark S. Woodrey, "Age-dependent foraging behavior of intercontinental bird migrants during stopover along the northern coast of the Gulf of Mexico."

Bethany L. Woodworth, "Dynamics of brood parasitism in a dry subtropical forest in Puerto Rico."

ROGER TORY PETERSON INSTITUTE TRAVEL AWARDS

Clint K. Miller, "Savannah Sparrow (*Passerculus sandwichensis*) responses to biennial changes in prey abundance, Delta Junction, Alaska."

D. S. Evered, "Climate and the Kirtland's Warbler, *Dendroica kirtlandii*."

ALEXANDER WILSON PRIZE (for best student paper)

Reed Bowman, "Influence of hatching asynchrony on reproductive patterns in the White-crowned Pigeon."

Selection committee for the Edwards Prize—Keith Bildstein, William Post, James Johnston, Peter Frederick, and Charles Blem, chair; for the Fuertes, Nice, and Stewart Awards—Richard Stiehl, Gary Nuechterlein, and Judy W. McIntyre, chair; for the Wilson Prize—Viki McDonald, Judy McIntyre, Craig Rudolph, and Dick Conner; for the Peterson Travel Award—Dick Conner, Paul A. Benke, and Lynn Moseley.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Banks at 08:35 on Friday 10 May in the Gardenia Room. Secretary Zimmerman summarized the highlights of Thursday's Council meeting. Next year the Society will meet with the Society of Canadian Ornithologists at the Univ. of Guelph, Guelph, Ontario from 29 April to 1 May. In 1994 the meeting will be at the Univ. of Montana, Missoula, Montana from 22 to 26 June in joint session with the Cooper Ornithological Society and The American Ornithologists' Union. The present membership is 2177 and reflects a slight increase over the last year. Charles Blem has been reelected as editor. The Publications Committee under the chair of Clait Braun presented a report that led to the decision that the designation of major papers in The Bulletin will be at the discretion of the editor and be based on content rather than the length of the study. All major papers,whether long or short, will be preceded by an abstract. Short Communications will not include an abstract. President Banks had appointed a new committee, the Undergraduate Outreach Committee chaired by Ernest Willoughby, which is charged with facilitating interest in ornithology among undergraduates by means of various mechanisms—

research support, faculty support, scholarships to attend summer field stations, and similar strategies. You are encouraged to communicate your ideas to the committee. Lastly, Zimmerman asked the membership to stand in honor of members who had died since the last annual meeting—Norman W. Bowers (Caledonia, NS), Mrs. William P. Cottrille (Jackson, MI), Ralph W. Dexter (Kent, OH), George A. Dorsey (Palmetto, GA), Gordon W. Gullion (Cloquet, MN), Mrs. John S. McCormick (Medford, OR), Russell T. Norris (Rockport, ME), Brian Obst (Los Angeles, CA), Elliot F. Porter (Albuquerque, NM), Dennis G. Raveling (Davis, CA), Edgar M. Reilly (Old Chatham, NY), Thane S. Robinson (Louisville, KY), Helmut Sick (Rio de Janeiro, Brazil), James O. Stevenson (Washington, DC), William Tallman, Jr. (Sewickley, PA), and William C. Vaughn (Niagara Falls, NY).

John Zimmerman presented the report of the nominating committee in the absence of Mary Clench, chair of the committee (additional members are William E. Davis, Jr., Fred E. Lohrer): Richard C. Banks, president; Richard N. Conner, first vice-president; Keith L. Bildstein, second vice-president; Doris J. Watt, treasurer; John L. Zimmerman, secretary; Laurie J. Goodrich, Janet G. Hinshaw, and John C. Kricher, two of whom will serve for a three-year term, 1992–1995, as councilors.

Doris Watt gave the treasurer's report.

REPORT OF THE TREASURER
1 January 1991 to 31 December 1991

GENERAL FUNDS

Balance Forward		$ 94,843.46
Receipts		
Regular and sustaining memberships	$ 20,549.00	
Student memberships	1,835.00	
Family memberships	600.00	
Total dues		$ 22,984.00
Subscriptions for 1991	$ 23,099.50	
Back issues	253.50	
Contributions from authors for page charges	22,420.00	
Total income from the Bulletin		$ 45,773.00
Contributions to The Van Tyne Library	$ 1,240.77	
Contributions to the Student Membership Endowment	30.00	
Contributions to the Wilson Award Endowment	105.00	
Contributions to General Endowment (Life Members, Patrons)	1,395.00	
Contributions to the Research Fund	161.00	
Contributions to the General Endowment	705.00	
Unrestricted contributions	154.00	
Total contributions		$ 3,790.77
Royalties		1,070.67
Interest from endowments		19,813.17
Dividends from Dreyfus account		4,447.31
List rental		1,458.06
Miscellaneous		419.34
TOTAL RECEIPTS		$ 99,756.32

Disbursements		
Bulletin Publication		
December 1990	$ 20,324.01	
March 1991	14,686.96	
June 1991	15,876.24	
September 1991	17,531.02	
Editor's expenses	5,450.00	
Total publication costs		$ 73,868.23
OSNA expenses	$ 16,522.00	
President's expenses	182.70	
Secretary's expenses	44.96	
Treasurer's expenses	226.34	
Treasurer's bond	100.00	
Bank charges (Canadian conversion, returned check)	20.27	
Editor's travel expenses	504.50	
Incorporation fee	8.00	
Student membership mailing list	169.80	
Application for PS Form 3510 to change address	90.00	
Printing and mailing of back issues	59.87	
Advertisement (Allen Press)	775.00	
Florida meeting advance funds	1,000.00	
Van Tyne Library	500.00	
AAZN dues	200.00	
Total operating expenses		$ 20,403.44
Organizational awards	$ 3,500.00	
Conservation reprints	1,378.75	
ICBP contributions	900.00	
Total philanthropies		$ 5,778.75
TOTAL DISBURSEMENTS		$100,050.42
Ending Balance		$ 94,549.36

CASH ACCOUNTS

First Source Bank checking account 31 December 1991	$ 16,853.95	
Dreyfus liquid assets 31 December 1991	77,695.41	
Total cash on hand		$ 94,549.36

DESIGNATED ACCOUNTS (Total Principals $87,545.63)

Fuertes & Nice Awards (Endowment Principal $10,000.00)

1991 Earnings*	$ 772.50
1990 Balance	500.00
Award funds available	1,272.50
Funds disbursed for awards	700.00
1991 Cash balance	572.50

Wilson Award (Endowment Principal $2,678.41)

1991 Earnings	$ 206.91
1989 Balance	(11.61)
Funds available	195.30

Funds disbursed for awards	100.00
1991 Cash balance	95.30

Stewart Award (Endowment Principal $22,649.90)

1991 Earnings*	$ 1,749.70
Funds disbursed for awards	800.00
1991 Balance	949.70

Edwards Prize (Endowment Principal $2,217.32)

1991 Earnings*	$ 171.29
Funds disbursed for awards	400.00

Sutton Color Plate Fund (Endowment Principal $50,000.00)

1991 Earnings*	$ 3,862.50
Funds disbursed for color plates 1991	3,268.00
Sutton Art Award	500.00
1991 Cash balance	94.50

* Based on 7.725% interest earned on $250,700.00 invested at the Mellon Bank.

GENERAL ENDOWMENT FUNDS

Balance of endowment principal 31 December 1990	$162,715.08
Balance of endowment principal 31 December 1991	$163,289.08

TOTAL ENDOWMENT FUNDS

1989 Principal	$250,585.00
Market value	$386,992.00
1990 Principal	$250,720.00
Market value	$372,063.00
1991 Principal (31 Dec 91)	$250,835.00
Market value (31 Dec 91)	$423,698.00

EDITOR'S REPORT—1991

In 1991, 170 manuscripts (68 major papers, 102 short communications) were received by *The Wilson Bulletin* editorial office. This is 24 more than in 1990. Of these, 51% were accepted, 40% were rejected, and 9% remain under review. Our acceptance rate over the past several years has been 58% for major papers and 44% for short communications. The time between receipt of manuscript from the author(s) and our return of the manuscript with referee comments nearly always has been less than three months. No manuscript required more than four months for a decision. There is not a great backlog of manuscripts, so accepted revisions almost always have been published in the next scheduled issue. Note, however, that there is an intrinsic four month delay in the process. For example, completed manuscript materials for the June issue must be submitted to Allen Press by approximately 15 February. The average time between receipt of a manuscript and its appearance in *The Wilson Bulletin* in 1991 was almost always less than a year. A few papers required longer because authors were slow in returning revisions.

Volume 103 was significant in several ways including, but not limited to, the appearance of a fold-out frontispiece, special book reviews, a frontispiece article in honor of Robert Mengel, and citation of our authors by several national publications, not the least of which was *The Wall Street Journal.* This volume was the fourth largest, in terms of total pages,

and appears to have been of appropriate size with regard to publication costs and available manuscript materials.

The editorial board—Kathy G. Beal, R. N. Conner, C. H. Stinson, and J. R. Walters—should be commended for their service to The Wilson Ornithological Society. They continue to give good advice and effective reviews. George A. Hall continues to oversee the production of book reviews in a timely, efficient manner. Assistant Editors Leann Blem, Albert E. Conway, and Anne Wenner are the major guardians of the style, format, and accuracy of the journal. I thank them for their efforts. Kathy G. Beal deserves special praise for continuing to assemble the index for *The Wilson Bulletin.* This is a tedious task and the entire society benefits from her careful work. Leann Blem and Robert Blem provide the manual labor that keeps the editorial office running and they watch over my shoulder to catch many of my errors. I thank the Wilson Society for continuing to have confidence in my editorship. As always, the editorial office is open to suggestions as to how to improve the service we provide the readers and authors.

C. R. Blem, *Editor*

The meeting was temporarily adjourned at 09:05 until the second session.

SECOND BUSINESS MEETING

President Banks opened the second business meeting at 13:32, Saturday, 11 April in the Gardenia Room.

President Banks recalled the report of the nominating committee to the floor of the assembly. Additional nominations from the floor were requested for the offices of president, first vice-president, second vice-president, treasurer, and secretary; but none were offered. George Hall moved and Tom Bancroft seconded that the nominations be closed. Clait Braun moved and Herb Kale seconded that a unanimous ballot be cast for this set of officers. The motion passed, and a unanimous ballot was duly recorded by the secretary. Ballots were passed out for the election of the two councilors, and after being properly counted it was subsequently announced that Janet G. Hinshaw and John C. Kricher had been elected.

REPORT OF THE RESOLUTIONS COMMITTEE

Peter Frederick presented the report of the resolutions committee.

Resolution on the Everglades Bioregion

WHEREAS, the Kissimmee-Okeechobee-Everglades basin contains one of the largest wetland ecosystems in eastern North America;

WHEREAS, the health and restoration of this system remains a national and international concern;

WHEREAS, because of drainage and degradation of these wetlands the number of water birds using the system has decreased over 90%;

WHEREAS, many plants, animals, and birds in this system have become rare, threatened, or endangered;

WHEREAS, the recovery of rare, threatened, and endangered species will require the restoration of these wetlands;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society (1) recommends that the Army Corps of Engineers and South Florida Water Management District proceed with the Level II backfilling plan for the restoration of the floodplain marshes of the Kissimmee River, (2) that water quality be restored to Lake Okeechobee and the Everglades to a level acceptable to the Outstanding Natural Resources Water designation found in

40CFR part 131.12, (3) that the natural timing, volume, and variation in water flow be restored to the Everglades marshes, and (4) that restoration ensure that a mosaic of natural vegetation with natural biodiversity be maintained.

The motion to accept this resolution was made by Clait Braun, seconded by Tom Imhof, and passed by the Society.

Resolution on Wetlands

WHEREAS, the United States has already lost more than half of its wetlands through drainage, destruction, and alteration;

WHEREAS, wetlands serve many important functions including flood protection, aquifer recharge, and pollution control;

WHEREAS, wetlands provide habitats for large populations of wildlife and fish species;

WHEREAS, wetlands provide important recreational and educational opportunities for people;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society recommends that (1) state and federal governments do all they can to protect and restore wetlands by increasing their rate of acquisition, protection, and restoration, (2) the Edwards bill, H.R. 4255, be adopted by Congress and that it continue to contain the following provisions: a) the Bush administration's currently proposed Wetlands Delineation Manual not be adopted, and that a study be commissioned to put wetland delineation on sound and credible scientific footing, b) that the Clean Water Act be further strengthened by expanding the range of wetland-destroying activities regulated by Section 404, by giving the EPA greater oversight and a more inclusive monitoring role in the general permit program as well as giving the Fish and Wildlife Service and the National Marine Fisheries Service more meaningful roles in commenting on Army Corps of Engineers permits.

It was moved by Mark Woodrey and seconded by Charles Smith to accept this resolution, and the motion passed.

Resolution on Florida's Preservation 2000

WHEREAS, Florida's natural environment contains a rich diversity of natural communities;

WHEREAS, Florida has one of the fastest growing human populations of any state in the nation;

WHEREAS, loss of natural areas in the state is progressing at an alarming rate;

WHEREAS, Florida can protect environmentally sensitive land through the implementation of the Preservation 2000 program;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society commends the Florida legislature for undertaking such a program and recommends that the Florida state legislature find a funding mechanism for the Preservation 2000 program that will provide money through the duration of the program.

It was moved by Richard Paul and seconded by Dick Conner to accept this resolution, and it passed.

Resolution on Endangered Species Reauthorization

WHEREAS, the Endangered Species Act will come up for reauthorization by Congress during 1992 or 1993;

WHEREAS, numerous species of plants and animals are threatened and endangered in the United States;

WHEREAS, recovery plans have not been developed for most of these species, or implemented for the majority of others;

WHEREAS, additional species are becoming endangered as destruction of habitat continues in the United States,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society recommends that the Endangered Species Act be reauthorized and strengthened through the adoption of the provisions in the Studds bill, H.R. 4045. Specifically, we recommend that (1) deadlines for the development and implementation of recovery plans be set, (2) priority be given to the development of integrated multispecies recovery plans for maintaining and restoring entire ecosystems or ecological communities, (3) multispecies recovery plans be developed that include candidate species as well as listed species, (4) citizens be authorized to file suit immediately in emergencies posing a significant risk to the well-being of an endangered species, (5) appropriate federal agencies be authorized to issue regulations to enforce and carry out the regulations and agreements in the Convention on International Trade in Endangered Species (CITES), (6) appropriations be increased for the Department of the Interior, the Department of Commerce, and the Department of Agriculture so that the Act can be implemented, and (7) a Habitat Conservation Planning Fund be established and funded.

It was moved by Charles Smith and seconded by Dick Conner to accept this resolution, and the motion passed.

Resolution to the Local Committee

WHEREAS, the 1992 meeting of the Wilson Ornithological Society, held jointly with a meeting of the Florida Ornithological Society, has been organized and executed in an extremely efficient manner;

WHEREAS, the receptions, field trips, and other activities of the 1992 meeting have provided a very unique and enjoyable experience for the attendees;

WHEREAS, the scientific program of the 1992 Wilson Ornithological Society has been extremely efficiently organized and executed, the papers of the scientific program have contributed significant new insights to the field of ornithology;

WHEREAS, the attendees of the meeting recognize that such results can have come only from a tremendous amount of time, hard work, and worry for the organizers, and recognize that these sacrifices of a few have led to the enjoyment and advancement of the entire society;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society (1) thanks the Florida Ornithological Society for inviting us to join them in Florida, (2) thanks Joe Jehl for arranging a truly unique and memorable reception at Sea World, (3) thanks all of the host organizations for allotting their resources for our benefit, (4) congratulates Keith Bildstein for his success in organizing and implementing the excellent scientific program, and (5) especially, congratulates Herbert Kale and the local committee on a job very well done, and thanks each one of the members of the local committee for their time, effort, and attention to detail which have made the meeting a great success.

President Banks called for a motion to accept this resolution and was met with a standing ovation, and proclaimed it passed by acclamation.

It was moved by George Hall to adjourn the meeting. It was seconded by Tom Bancroft. And the meeting was adjourned.

The reports of the standing committees are as follows.

REPORT OF JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE—1991

It can't be, yet it is, the end of another calendar year of our Library's activity. The mere listing of names and figures is quite inadequate, as usual, to indicate all the business that has been transacted and services rendered, and much less the day-to-day work, including recordkeeping and correspondence, that is entailed, or the dedication and generosity of the many here and elsewhere who have participated.

Janet Hinshaw of the University of Michigan Museum of Zoology Bird Division, still basically in charge of operations, routine and otherwise, continues her long and meritorious service. She, in turn, wished to acknowledge the splendid assistance given in the past year by Susan Morseau, secretary in the Bird Division, and Stephanie Buus and Katie Beltaire, student assistants.

It certainly appears that satisfactory progress is being made in various directions. Among the statistics that follow, most compare favorably with those of previous years, and in certain instances large increases are evident.

Direct contributions by 23 members and from other sources have added 3334 items to our collections: 35 books, 68 monographs and reports, 167 reprints, 3065 journal issues (most of these from Harrell Books), and monetary donations to our New Book Fund. Contributors include J. L. Atwood, A. J. Berger, R. C. Banks, R. Bayer, G. W. Hall (WOS review copies), K. W. Haller, Harrell Books, J. Hinshaw, R. Hoffman, V. W. Inman, W. D. Middleton, T. Milney, M. K. McNicholl, Oklahoma Ornithological Society Library, R. B. Payne, A. R. Phillips, Point Reyes Bird Observatory, W. Post, S. Violani, H. Wing, D. S. Wood (Carnegie Museum), and J. L. Zimmerman.

From the New Book Fund, $292.20 was spent for the purchase of four books and nine monographs. The fund was augmented by receipts of $1551.76 through the sale of 202 duplicate books. Such sale is often limited by the inconvenience of adequate promotion at otherwise appropriate times and places.

In all, 216 journal titles were received, including 171 by exchange with 129 institutions and individuals, 32 as gifts from 26 such sources, and 13 through direct subscription with 11 institutions. These figures tend to fluctuate a bit from year to year as particular situations change. In 1991, $233.40 was spent for direct subscription costs.

The exchanges we make with other institutions, we perceive not only as a means to increase our own holdings, but also as a valuable way to extend the circulation of the "Bulletin" into all parts of the world, with many obvious advantages to all concerned.

And further evidence of the ultimate value of any and all donated materials, several hundred duplicate journal issues were this year donated to museums and libraries in various countries, including Mexico, Brazil, the Philippines, and Uganda.

In 1991, 142 loan items and 254 photocopies of articles were supplied to 40 members and libraries in 72 transactions. Always, there is a steady flow of ornithologists and other scientists, students, and laymen (members and nonmembers) who put our fine collection or literature to on-the-spot use here in Ann Arbor.

Members are always encouraged, whenever possible, to make fuller use of our growing WOS library facilities; as the occasion permits, they can reciprocate with contributions of their own. It becomes more and more clear that we in the Library and in the Society are all part of a worldwide continuum, fostering the dissemination of ornithological knowledge.

William A. Lunk, *Chair*

REPORT OF THE CONSERVATION COMMITTEE

The Conservation Committee was asked to prepare a list of conservation policy issues for which the Wilson Ornithological Society as a scientific organization should develop a position. Although there is no shortage of worthy and critical concerns upon which the Society might have some impact, the committee attempted to provide a list of policy issues that affect many species (avian or otherwise) rather than focus on species-specific problems. The committee also considered policy matters that may affect future ornithological research programs.

Because these policy issues were intended to be suggestions for more thorough study by future Conservation Committees or other appointed groups, this committee did not elaborate greatly on any single topic. Instead, an attempt was made to provide a concise statement of each problem and to suggest potential action that the Wilson Ornithological Society might take in further defining the critical issues or developing a policy.

The Committee was aware that the Executive Council will decide which, if any, of these topics to pursue in greater detail, but felt that it was within its charge to emphasize certain issues deemed to be the most important. Accordingly, the first three issues presented below were deemed of critical importance by the Conservation Committee. We urge the Executive Council of the WOS to take immediate action on these issues and to join national coalitions in support of these efforts.

The remainder of the issues suggested by the Conservation Committee are no less important but do not require immediate action. Any or all of these issues could become the focus of an in-depth report by a future committee. These issues are listed randomly; no significance should be placed upon their position in the list.

Issues of Immediate Importance

Reauthorization of the Endangered Species Act. The Society should strongly support the reauthorization of the Endangered Species Act. The Society might play a vital role in deflecting efforts to weaken the valuable provisions of the Act by finding ways to suggest broader participation in recovery planning and habitat conservation plans.

National Wetlands Legislation. The Society should resist efforts to weaken existing wetlands legislation. The Society should use the report of the past Conservation Committee as a building block to suggest wetland definitions that will protect ecologically important habitats but reduce the problems caused by overzealous regulators with little ecological training or common sense. The Executive Council should examine the stance taken by The Wildlife Society on this issue and make similar efforts.

Funding of the Nongame Wildlife Act. Congress passed this Act in 1978 but has never supported it with appropriations. The Society should review this legislation and suggest research and funding priorities. The Society should undertake a lobbying effort to obtain funding for this legislation.

Other Issues of Importance

Biodiversity Protection in both Tropical and Temperate Zones. The Society should examine land management practices in tropical and temperate environments. This effort should be directed towards protecting essential habitats by developing a treaty with all the destination countries of migratory birds in this hemisphere.

Support for Contamination Studies. Current levels of support for contaminants research has slipped below funding levels of the past decade. The Society should appoint a committee to review research and development needs in this field of research. The committee might also examine the current research efforts in biological pest control.

Education Programs. Project Wild has been an exceptionally successful program in introducing school-age children to nature. Since a higher percentage of our population is becoming urban-centered, the Society should examine methods of educating children about birds and nature. A committee might be appointed to review existing educational schemes and suggest ways in which ornithologists and birders might assist.

Illicit Pet Trade; Smuggled Birds. The Society should develop a strong policy statement about the illicit pet trade. A committee should examine the scope of the problem and suggest ways that the avian pet industry could be regulated to reduce the import of illegally obtained birds.

Protection for the Arctic National Wildlife Refuge. Although drilling in the ANWR has

been recently removed from the Senate version of the national energy bill, the Society should make a statement about the value of this refuge to wildlife.

Support for General Collecting Permits. A number of state wildlife agencies have adopted policies that have effectively eliminated "opportunistic" collecting by ceasing to issue general collecting permits. Although collecting permits for specific research projects may still be issued by these states, the state agencies have acted to disallow documentation of occurrences by specimen collections. The Society should take a stand on this issue because of the potential impact on future research and museum efforts. Perhaps a committee could review the role of scientific collecting in the modern context and suggest guidelines that state wildlife agencies could use to establish policies for collecting permits.

Support for Museum Collections. The Society should consider developing a policy statement that emphasizes the importance of governmental support for the curation and expansion of specimen collections.

Brown-headed Cowbird Control. Although there are many factors contributing to the decline in eastern populations of migratory birds, the effect Brown-headed Cowbirds can have on small populations has been demonstrated in such endangered species as the Kirtland's Warbler and Black-capped Vireo. It has been implicated as a major factor in the declines of other species as well. The Society should review the literature on cowbird control, and develop a policy regarding its use.

Brian R. Chapman, *Chair*

REPORT OF THE MEMBERSHIP COMMITTEE

As the membership committee chair, I receive a few inquiries each month; about half of these are from persons interested in joining. To each I send our membership brochure and a personal letter welcoming them to the Society. I also receive inquiries regarding institutional subscriptions, and answer those letters accordingly. Not infrequently I am contacted by a member who is not receiving copies of the *The Wilson Bulletin.* These matters are brought to the attention of OSNA Director, Fred Lohrer, and I follow that up by corresponding with the (temporarily, I hope) unhappy member.

Herb Kale kindly arranged delivery of the WOS membership poster to me at the RRF meeting in Tulsa last November, where it was displayed. Unfortunately, after a couple of days only about 10 brochures were picked up.

The WOS passively participated in AFO's campaign to garner more institutional subscriptions for the four OSNA journals; each society paid a fourth of the cost of the mass mailing. Greg Butcher, AFO membership chair, should be applauded for his efforts.

In regard to our own mass mailing directed at OSNA members who are not also members of the WOS, I decided it would be desirable to address personally each recipient of the letter of invitation to join. To that end, the names, addresses, and salutations for 2467 potential U.S. and Canadian members were typed into a file to be used for merging the letters. We plan to begin producing the letters in the near future, and I will seek advice from Fred Lohrer and/or Greg Butcher on how best to accomplish the mailing.

It was suggested to me that Allen Press could include a WOS membership form with its shipments of *Wilson Bulletin* reprints. I will discuss the feasibility, cost, and expected returns with Fred.

John A. Smallwood, *Chair*

The Committee on Scientific Program composed of Keith Bildstein, chair, Richard N. Conner, and John W. Fitzpatrick presented the following paper session, facilitated by session

moderators Keith Bildstein, Margaret C. Brittingham, Robert L. Curry, John W. Fitzpatrick, Peter C. Frederick, Danny J. Ingold, Dan Klem, M. Victoria McDonald, J. D. Rising, and Rebecca B. Smith.

PAPERS SESSIONS

Eduardo E. Iñigo-Elias, Dept. Wildl. & Range Sci., Univ. Florida, Gainesville, FL. "Ecology, biology, and conservation of the Scarlet Macaw (*Ara macao*) in the Selva Lacandona region of Chiapas, Mexico."

R. Terry Chesser, Mus. Nat. History, Louisiana St. Univ., Baton Rouge, LA. "An overview of austral migration in South America."

Mark S. Woodrey, Dept. Biol. Sci., Univ. S. Mississippi, Hattiesburg, MS. "Stopover biology of autumnal landbird migrants along the northern coast of the Gulf of Mexico."

Reuven Yosef, Dept. Zoology, Ohio State Univ., Columbus, OH, James N. Layne and Fred E. Lohrer, Archbold Biol. Sta., Lake Placid, FL. "Trends in the numbers of Loggerhead Shrikes in peninsular Florida, 1974–1989."

Rebecca B. Smith and David R. Breininger, The Bionetics Corp., Kennedy Space Center, FL. "Feeding habitat use by wading birds on Kennedy Space Center."

Courtney J. Conway, Dept. Nat. Resource Sci., Univ. Rhode Island, Kingston, RI, and Thomas E. Martin, Arkansas Coop. Fish and Wild. Res. Unit., Univ. Arkansas, Fayetteville, AR. "Habitat suitability for Williamson's Sapsuckers in mixed-conifer forests."

William R. Eddleman and Ronald E. Flores, Dept. Nat. Resource Sci., Univ. Rhode Island, Kingston, RI. "Habitat use by the California Black Rail in southwestern Arizona."

Kenneth D. Meyer and Steven M. McGhee, Dept. Wildl. & Range Sci., Univ. Florida, Gainesville, FL. "GIS and radio-tracking analysis of nesting and foraging habitat selection by American Swallow-tailed Kites in Florida."

Charles E. Yohn, Grad. Prog. Ecology, Penn. State Univ., University Park, PA. "The effect of size and shape of forest clearcut stands on breeding bird communities in a northern hardwood forest."

D. E. Evered and L. R. Messick, Dept. Biol. Sci., Florida State Univ., Tallahassee, FL. "Climate and the Kirtland's Warbler (*Dendroica kirtlandii*)."

Robert E. Bennetts, Dept. Fish. & Wildl. Biol., Colorado State Univ., Ft. Collins, CO. "Associations among dwarf mistletoe, snags, and cavity-nesting birds in ponderosa pine stands in Colorado."

T. Scott Sillett, Mus. Nat. Sci., Louisiana St. Univ., Baton Rouge, LA. "Bird use of epiphytes in the montane rainforests of Costa Rica."

George L. Weymouth, Florida Dept. Nat. Resources, Tallahassee, FL. "Comparison of waterbird abundance and activity on two exotic plant species."

David S. Lee, North Carolina State Mus., Raleigh, NC. "Manx Shearwaters off the southeastern U.S. coast."

J. D. Rising, Dept. Zoology, Univ. Toronto, Toronto, ON. "Geographic variation in size of Savannah Sparrows (*Passerculus sandwichensis*)."

Jon Barlow and Anthony Lang, Dept. Ornithol., Royal Ont. Mus., Toronto, ON. "Range extension of the Eurasian Tree Sparrow and the first hybrid Eurasian Tree × House Sparrow in North America."

Nedra K. Klein, Robert B. Payne, and Laura L. Payne, Mus. Zool., Univ. Michigan, Ann Arbor, MI. "A molecular perspective on speciation in the brood parasitic *Vidua* finches."

Richard C. Banks, Biol. Surv., U.S. Fish & Wildlife Service, Washington, DC. "The correct generic name for the Crested Caracara(s)."

Richard R. Schaefer, Richard N. Conner, and D. Craig Rudolph, S. Forestry Exper. Sta.,

Nacogdoches, TX. "Provisioning of nestlings and fledging success of Red-cockaded Woodpeckers in relation to habitat."

C. K. Miller, R. L. Knight, and L. C. McEwen, Dept. Fish and Wildl., Colorado St. Univ., Ft. Collins, CO. "Savannah Sparrow (*Passerculus sandwichensis*) responses to biennial changes in prey abundance, Delta Junction, Alaska."

Jeff P. Smith, Dept. Wildl. and Range Sci., and Marilyn G. Spalding, Dept. of Infect. Diseases, Univ. Florida, Gainesville, FL. "Growth and survival of nestling Great Egrets infected by the nematode *Eustrongylides ignotus*."

Reed Bowman, Dept. Biology, Univ. South Florida, Tampa, FL. "Influence of hatching asynchrony on reproductive patterns in the White-crowned Pigeon."

Daniel R. Kozlovic, Dept. Zoology, Univ. Toronto, Toronto, ON. "Selection for host avoidance in the Brown-headed Cowbird (*Molothrus ater*)."

David L. Leonard, Dept. Biology, Univ. Central Florida, Orlando, FL. "Monthly variation in Loggerhead Shrike caches in central Florida."

Barnaby N. Marsh, IV, Harvard Univ., Cambridge, MA. "Competition between Black Vultures and Turkey Vultures: a factor influencing mixed roosts?"

Andrew W. Kratter, Mus. Nat. Sci., Louisiana St. Univ., Baton Rouge, LA. "Geographic variation in *Cacicus holosericeus,* a partial bamboo specialist."

Anthony L. Lang, Dept. Zoology, Univ. Toronto, Toronto, ON. "Mechanisms of cultural evolution in song pools in a unidirectionally expanding population of the Eurasian Tree Sparrow."

Petra Bohall-Wood, Dept. Wildl. & Range Sci., Univ. Florida, Gainesville, FL. "Post-fledging ecology and survival of fledgling Bald Eagles."

John A. Smallwood, Dept. Wildl. & Range Sci., Univ. Florida, Gainesville, FL, and Michael W. Collopy, Pacific Forest and Rangeland Systs. Coop. Res. Unit, Forest Sci. Lab., Corvallis, OR. "American Kestrels breeding in two habitats in Florida: differential responses to a large increase in nest site availability."

Timothy Brush, Dept. Biology, Univ. Texas–Pan American, Edinburg, TX. "Responses of House Wrens and Prothonotary Warblers to nest boxes in a flooded riparian forest in Iowa."

Brian K. Mealey, Falcon Batchelor Bird of Prey Center, Miami Mus. Sci., Miami, FL, and George Dalrymple, Florida Internat. Univ., Miami, FL. "Reproductive ecology of the Burrowing Owl, *Athene cunicularia floridana,* in Dade and Broward counties, Florida."

Peter C. Frederick, Robin Bjork, G. Thomas Bancroft, and George Powell, National Audubon Soc., Tavernier, FL. "Consequences of coastal locations on reproduction of dayherons in southern Florida."

Wayne Norling, Center for Wetland Resources, Louisiana St. Univ., Baton Rouge, LA, and James Allen, U.S. Fish & Wildl. Ser., Lafayette, LA. "Nest site characteristics of American Swallow-tailed Kites in Louisiana and Mississippi."

Ralph D. Morris, Dept. Biol. Sci., Brook Univ., St. Catherines, ON, and John W. Chardine, Canadian Wildl. Serv., St. John's, Newfoundland. "Recent trends in breeding and survival of Brown Noddies nesting near Culebra, Puerto Rico."

Charles R. Blem and Leann B. Blem, Dept. Biology, Virginia Commonwealth Univ., Richmond, VA. "Composition and microclimate of Prothonotary Warbler nests."

Michael Stoskopf, College Vet. Medicine, North Carolina State Univ., Raleigh, NC, and Lynn A. Mahaffy, Dept. Nat. Resources, Cornell Univ., Ithaca, NY. "Some effects of disturbance upon the growth rates of Common Puffin (*Fratercula arctica*) chicks."

Curtis S. Adkisson, Dept. Biology, VPI & SU, Blacksburg, VA. "Partitioning of the cavity resources in a Colorado aspen forest."

Lawrence H. Walkinshaw, Lake Wales, FL. "Nesting records of the Florida Sandhill Crane."

J. Edward Gates, Appalachian Environ. Lab., Frostburg, MD. "Patterns of breeding bird assemblages on altered forest landscapes in the central Appalachians."

John W. Fitzpatrick, Glen E. Woolfenden, and Robert L. Curry, Archbold Biol. Sta., Lake Placid, FL. "Recent burns as shifting resources in the landscape ecology of Florida Scrub Jays."

R. Todd Engstrom, Tall Timbers Res. Sta., Tallahassee, FL, and Frances C. James, Dept. Biol. Sci., Florida State Univ., Tallahassee, FL. "Fire ecology and birds in longleaf pine ecosystems."

Richard L. Hutto, Dept. Biol. Sci., Univ. Montana, Missoula, MT. "The uniqueness of early post-fire bird communities in Rocky Mountain coniferous forests."

John L. Zimmerman, Div. Biology, Kansas State Univ., Manhattan, KS. "Tallgrass prairie birds and the red buffalo."

Michele E. Hannon and Robert L. Curry, Dept. Biology, Villanova Univ., Villanova, PA. "Why is unburned habitat suboptimal for Florida Scrub Jays?"

Scott R. Klinger, USDA Forest Service, Atlanta, GA, Ronald E. F. Escano, USDA Forest Service, Asheville, NC, Dawn E. Carrie, USDA Forest Service, Cleveland, TX, and Gilbert Zepeda, USDA Forest Service, Rio Piedras, PR. "The Sister Forest Program: a partnership to conserve neotropical migratory birds."

Jerome A. Jackson, Dept. Biology, Mississippi State Univ., Mississippi State, MS. "Plumages and molt of the Red-cockaded Woodpecker."

Deborah K. Jansen and Kenneth D. Meyer, Big Cypress Natl. Preserve, NPS, Ochopee, FL. "Radio-tracking study to assess a decline in Red-cockaded Woodpeckers."

Danny J. Ingold, Dept. Biology, Muskingum College, New Concord, OH, and Robin J. Densmore, New Concord, OH. "Influences of starling harassment for nest sites on three woodpecker species."

Jack P. Hailman, Univ. Wisconsin, Madison, WI, Kevin J. McGowan, Cornell Univ., Ithaca, NY, and Glen E. Woolfenden, Univ. S. Florida, Tampa, FL. "The role of helpers in the sentinel behavior of Florida Scrub Jays."

Kelly J. Goocher, Univ. Florida, Gainesville, FL, Michael Avery, USDA-Aphis, Denver Wildl. Research Sta., Gainesville, FL, and Marsha A. Cone, Univ. Florida, Gainesville, FL. "Berry size selection and blueberry crop damage by Cedar Waxwings."

D. Craig Rudolph, Richard N. Conner, and Richard R. Schaefer, S. Forest Exper. Sta., Nacogdoches, TX. "Foraging behavior of post-fledging Red-cockaded Woodpeckers."

Richard N. Conner and D. Craig Rudolph, S. Forest Exper. Sta., Nacogdoches, TX. "Possible stabilization of a small declining Red-cockaded Woodpecker population in Texas."

Daniel Saenz, Richard N. Conner, and D. Craig Rudolph, S. Forest Exper. Sta., Nacogdoches, TX. "Some methods for measuring habitat loss and fragmentation for Red-cockaded Woodpeckers in southern national forests."

Shirley J. Burgdorf, D. Craig Rudolph, Richard N. Conner, and Richard R. Schaefer, S. Forest Exper. Sta., Nacogdoches, TX. "Composition of mixed species foraging flocks associated with Red-cockaded Woodpeckers."

Joseph R. Jehl, Hubbs-Sea World Res. Institute, San Diego, CA. "The night the birds fell: the physiology of a wreck of Eared Grebes."

Dennis L. Krusac, USDA Forest Service, Atlanta, GA, Ronald E. F. Escano, USDA Forest Service, Asheville, NC, Joseph M. Dabney, and John J. Petrick, USDA Forest Service, Atlanta, GA. "Proposed ecosystem management for recovering the Red-cockaded Woodpecker on southern national forests."

Eduardo E. Iñigo-Elias, Dept. Wildl. & Range Sci., Univ. Florida, Gainesville, FL, and Michael W. Collopy, Pacific Forest and Rangeland Systs. Coop. Res. Unit, Forest Sci. Lab., Corvallis, OR. "Community structure and ecological correlates of forest fragmen-

tation and habitat alterations on a tropical raptor assemblage in the Selva Lacandona region of Chiapis, Mexico."

Frances C. James, Dept. Biol. Sci., Florida State Univ., Tallahassee, FL, and David A. Wiedenfeld, Mus. Nat. Sci., Louisiana State Univ., Baton Rouge, LA. "Hotspots of decline in a landscape of generally increasing populations of North American Birds."

David Klem, Jr., David C. Keck, Karl L. Marty, Amy J. Miller, and Cory T. Platt, Dept. Biol., Muhlenberg College, Allentown, PA. "Preventing avian mortality at windows by angling glass and feeder placement."

Margaret C. Brittingham and Jeffrey P. Hoover, School Forest Resources, Pennsylvania State Univ., University Park, PA. "Regional variation in cowbird parasitism of Wood Thrush."

David L. Fischer, Agric. Div., Miles Inc., Stillwell, KS, and Louis B. Best, Dept. Animal Ecol., Iowa State Univ., Ames, IA. "Field measurement of avian exposure to pesticide granules."

M. Victoria McDonald, Dept. Biology, Univ. Central Arkansas, Conway, AR. "New technological advances in bird song analysis."

Richard L. West, Tallahassee, FL, and Gene K. Hess, Delaware Mus. Nat. History, Wilmington, DE. "Trends in the populations of birds in eastern United States in winter."

James Cox, Florida Game and Fresh Water Fish Comm., Tallahassee, FL. "Effects of land-cover composition on breeding bird surveys in Florida."

Douglas A. James, Dept. Biol. Sci. and Barbara A. Raulston, Arkansas Coop. Fish and Wildl. Res. Unit, Univ. Arkansas, Fayetteville, AR. "Do cavity restrictors affect bill length in Red-cockaded Woodpeckers?"

James A. Sedgwick, Natl. Ecol. Res. Ctr., Fort Collins, CO. "Leg injury to Willow Flycatchers as a consequence of color banding."

POSTERS

Satu Pernanen, Dept. Zool., Univ. Toronto and Jon Barlow, Ornithol. Dept., Royal Ontario Mus., Toronto, ON. "Nest-site characteristics of sympatric Brewer's Sparrows and Clay-colored Sparrows."

David R. Breininger, Vickie L. Larson, Brean Duncan, Rebecca B. Smith, and Donald M. Oddy, Bionetics Corp, Kennedy Space Ctr., FL. "Habitat and territory attributes of the Florida Scrub Jay in a coastal pine flatwoods using a Geographic Information System (GIS)."

Mary C. Crowe, Louis B. Best, James P. Gionfriddo, Dept. Animal Ecol., Iowa State Univ., Ames, IA, and David L. Fischer, Agr. Div. Miles Inc., Stillwell, KS. "Avian nest-site selection and nesting success in two Florida citrus groves."

ATTENDANCE

ALABAMA: *Birmingham,* Thomas A. Imhof.

ARKANSAS: *Conway,* M. Victoria McDonald; *Fayetteville,* Douglas A. James, Barbara Raulston.

CALIFORNIA: *San Diego,* Joseph R. Jehl.

COLORADO: *Fort Collins,* Clait E. Braun, Clinton K. Miller, Jim Sedgwick; *Longmont,* John W. Prather.

DISTRICT OF COLUMBIA: Chuck Banks, Richard C. Banks, Roger B. Clapp.

FLORIDA: *Altamonte Springs,* Greg Bretz; *Archer,* Marilyn G. Spalding; *Bartow,* Mae Hartsaw; *Boca Raton,* Sheila A. Mahoney; *Cocoa,* David Simpson; *Fort Pierce,* Jane Brooks; *Gainesville,* Alfredo J. Begazo, Christine Champe, Peter C. Frederick, Kelly J.

Goocher, John W. Hardy, Eduardo Iñigo-Elias, Diana Matthiesen, Steven M. McGehee, Ken Meyer, Karl Miller, Joan L. Morrison, James A. Rodgers, John A. Smallwood, Jeff P. Smith, Ruthe Smith, Dan Wenny, Petra Bohall-Wood; *Hobe Sound,* Peter G. Merritt, Victoria L. Merritt; *Hollywood,* Jocie Baker; *Homestead,* John Curnutt, William B. Robertson, Jr., P. William Smith, Susan A. Smith; *Jacksonville,* Mary Davidson, Cheryl Evans, Cherie Irby, Peggy Powell; *Kennedy Space Center,* David Breininger, Ron Schaub, Rebecca B. Smith; *Key West,* Joseph A. Ondrejko; *Lake City,* Cynthia Thompson; *Lakeland,* Bobbie Kittleson; *Lake Placid,* Reed Bowman, John W. Fitzpatrick, Fred E. Lohrer, Bill Pranty, Reuven Yosef; *Lake Wales,* Skip Huxtable, Diane Pierce, Clara Walkinshaw, Larry Walkinshaw; *Lehigh Acres,* Ben Kiff, Maxine Kiff; *Melbourne,* Jim Angy, Bob Brown, Edward Slaney, Marie Slaney, Tami Townsend; *Miami,* Brian Mealey; *Moore Haven,* Ursula Feller, June McCallum; *Ocala,* Julie Hovis; *Ochopee,* Rob Bennetts, Deborah Jansen; *Okeechobee,* Scott Hedges; *Orlando,* Herbert W. Kale II, David Leonard, Becky Payne, Christine R. Rucker, Eric Stolen, Walter K. Taylor; *Ormond Beach,* Daniel Ambrose; *Pembroke Pines,* Tim Towles; *Port Charlotte,* Malcolm M. Simons, Jr.; *Quincy,* Doug Runde; *St. Augustine,* Ann Pearrow, Thomas N. Pearrow; *St. Cloud,* Marty Folk; *St. Petersburg,* David Goodwin, Lee Snyder; *South Pasadena,* Neal Adamson; *Tallahassee,* W. Wilson Baker, Jim Cox, R. Todd Engstrom, Duncan S. Evered, Frances James, Lyla R. Messick, Katy Nesmith, Rick West, George Weymouth; *Tampa,* Eva Bailey, Martha Mandlow, Samuel Mandlow, Richard T. Paul, Tony Steffer, Keith Tarvin, David K. Voights; *Tavernier,* Thomas Bancroft, Robin Bjork; *Venus,* Glen E. Woolfenden, Janet Woolfenden; *West Palm Beach,* Elwood D. Bracey, Yvonne Hughes, Cynthia Plockelman; *Winter Haven,* Buck Cooper, Linda Cooper, Helen Eastman, Tom Palmer; *Winter Park,* Bruce H. Anderson, Wes Biggs, B. B. Biggs, Parks Small, Eugene Stoccardo.

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ANNOUNCEMENTS

THIRD INTERNATIONAL CONFERENCE, THE EFFECTS OF OIL ON WILDLIFE. January 27–29,1993. New Orleans, Louisiana. This multi-disciplinary meeting will serve industry, government, veterinarians, researchers and rehabilitators, and will focus on contingency planning, wildlife response and research. Presented by: Tri-State Bird Rescue and Research, Inc. Through a grant from: Clean Gulf Associates. For more information contact:

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CALL FOR PAPERS

The U.S. Fish and Wildlife Service is sponsoring a symposium of the ecology, restoration, and management of prairie wetlands, August 9–13, 1993. The symposium will be hosted by Northern Prairie Wildlife Research Center in Jamestown, North Dakota. The symposium will feature 2½ days of technical sessions, an evening poster session, and an afternoon of field demonstrations. Optional field trips of prairie habitats, fauna, and management activities will be available 9–10 August for interested individuals. Abstracts of accepted papers will be printed and distributed at the symposium. There will be no published proceedings. Completed titles forms for papers or posters should be mailed to arrive by 1 Jan. 1993 and authors will be notified of acceptance by 1 Feb. 1993. Those interested in submitting paper/poster titles or attending the symposium should contact: Dr. Ned H. Euliss, Jr., U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Route 1, Box 96C, Jamestown, North Dakota 58401-9736. 701/252-5363.

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Editor Charles R. Blem
Department of Biology
Virginia Commonwealth University
816 Park Avenue
Richmond, Virginia 23284-2012

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Review Editor George A. Hall
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West Virginia University
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